CHAPTER 1-2
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 1

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AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 1

Figure 1. Alpine tundra lake, late snowbeds, and small streams where some members of the **Cephaloziineae** may take advantage of the longer availability of moisture. Photo courtesy of Bob Janke.

Nomenclature for the liverwort subchapters is based on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

As in the subchapter on **Anthocerotophyta**, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I searched in Google Scholar for additional information on the species in that constructed list. I do not pretend that this is complete. It concentrates on streams, but includes lakes and other wetlands. It deliberately ignores bogs and mostly ignores fens, but nevertheless includes a few of these species because they were found in one or more other wetland studies. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the stream habitats with which I am most familiar, should be given priority.

I have thus far found no records of **Haplomitriopsida** in these studies. Hence I have not included that class in this chapter. Söderström *et al*. (2016) list 5 suborders in the order **Jungermanniales** of the **Jungermanniopsida**. This subchapter includes the suborder **Cephaloziineae**. In that suborder, most of the species outside the **Scapaniaceae** are only marginally associated with water. Although many of the species in the **Cephaloziineae** are not typical wetland or aquatic species, those included here were, nevertheless, found in a wetland or aquatic study. Their relative frequency can be noted based on the number of references cited.

The human propensity for trying to pigeon-hole members of a continuum is no more obvious anywhere than it is among "aquatic" bryophytes. Not only do they not pigeon-hole into neat habitat categories, the species tend to have wide physiological and at least some morphological variance, causing them to be named as multiple species when they are in fact environmental variations of one species. I have included the synonyms that I found in the aquatic literature, but many additional ones often exist.

Adelanthaceae

Only two members of this family appeared in my search for wetland and aquatic studies. These both occur in tropical regions where few studies are available regarding their ecology.

Cuspidatula flexicaulis (see Figure 3)

(syn. = *Jamesoniella balansae*, *Jamesoniella flexicaulis*, *Jamesoniella affinis* fo. *minor*)

Distribution and Wet Habitats

Cuspidatula flexicaulis (see Figure 2-Figure 3) is distributed in Malaysia, Indonesia, Papua New Guinea, and New Caledonia (GBIF 2020a). Ruttner (1955) listed it among the wetland and aquatic species in the tropics. In New Zealand it is an abundant species in subalpine forests (Scott 1970).

Figure 2. ***Cuspidatula monodon***; ***Cuspidatula flexicaulis*** is a species that sometimes occurs in wetlands. Photo by David Tng, with permission

Figure 3. ***Cuspidatula monodon***; ***Cuspidatula flexicaulis*** is a species that sometimes occurs in wetlands. Photo by David Tng, with permission.

Syzygiella sonderi (Figure 4)

(syn. = *Cryptochila grandiflora*)

Distribution

Syzygiella sonderi (Figure 4) is a widespread species, occurring in the Southern Hemisphere, including high elevations in the Neotropics (southeastern Brazil, tropical Andes, and Central America) (Gradstein & da Costa 2016). In the Eastern hemisphere it occurs on Réunion Island in the Mascarenes and in New Guinea and Borneo (Váňa *et al*. 2014).

Figure 4. ***Syzygiella sonderi***, a Southern Hemisphere species that benefits from high water levels of mountain streams. Photo by Juan Larrain, through Creative Commons.

Aquatic and Wet Habitats

In the Andes, Gradstein *et al*. (2018) listed ***Syzygiella sonderi*** (Figure 4) as a submerged liverwort from higher elevation lakes. In the northern maritime Antarctic it occurs on heated ground on volcanic islands. It is positively correlated with bankfull discharge in 48 streams on South Island, New Zealand (Suren & Duncan 1999); Lepp (2012) found it associated with steep streams in high rainfall areas on South Island. Nevertheless, on sub-Antarctic Marion Island this species occurs in **feldmark** (plant community characteristic of sites where plant growth is severely restricted by extremes of cold and exposure to wind, typical of alpine tundra and sub-Antarctic environments) in dry situations, typically associated with other bryophytes. In the Antarctic region, ***Syzygiella sonderi*** occurs on volcanic ash and debris, on rock ledges, and on gravel in protected moist areas (Bednarek-Ochyra *et al*. 2000).

On Marion and Prince Edward Islands, the mire drainage line peats are less acidic, and with higher Ca and Mg concentrations than peats of other mire habitats (Chown & Froneman 2008). On the more mineral soils, ***Syzygiella sonderi*** (Figure 4) is restricted to mire drainage lines, where it is one of the dominant species.

Adaptations

Syzygiella sonderi (Figure 4) has a moderate or low optimum for photosynthetically active radiation (PAR) and low photoinhibition, while also having high photoprotective capability when desiccated, characteristics that are beneficial at high elevations (Tonkie 2016). Nevertheless, it has only moderate photosynthetic capacity with low effective quantum yield and relatively low photoprotective capability. This species achieves its moderate photosynthetic rate at a moderate optimal PAR and has low to moderate response to light at low levels. Photochemistry ceases at moderate to very high **relative water content** [RWC; RWC = ((fresh mass-dry mass)/(saturated mass-dry mass)) × 100]. Nevertheless, it has high ability to recover its photochemistry upon rehydration.

Anastrophyllaceae

Anastrophyllum assimile (Figure 5)

Distribution

Anastrophyllum assimile (Figure 5) is widespread in Asia, Europe, and North America, and extends to Malesia. Known locations include Austria, Switzerland, Italy, Norway, Alaska, Yukon, British Columbia, Labrador, Greenland, Japan, Korea, Borneo, and Papua New Guinea (Schill & Long 2003). It is an alpine species, extending down into the montane *Abies-Rhododendron* forests. In the Upper Bureya River (Russian Far East), where it is rare, it occurs on wet cliffs (Konstantinova *et al*. 2002). In Arctic and alpine areas of North America, this species is associated with **siliceous** (containing or consisting of silica) substrates (Horton 1977).

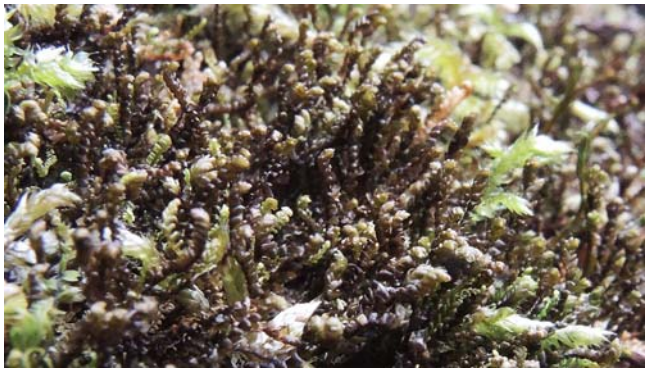

Figure 5. ***Anastrophyllum assimile***, a Northern Hemisphere species that can occur on wet cliffs and submergence areas around lakes and other wet areas. Photo by Kristian Hassel, through Creative Commons.

Aquatic and Wet Habitats

Anastrophyllum assimile (Figure 5) occurs in wet cliff crevices along the shoreline of Takakia Lake, Queen Charlotte Islands, British Columbia, Canada (Hong 2007). It is among the numerous rare species that are vulnerable to changes in lake water level, including also the rare and unusual ***Takakia lepidozioides*** (Figure 6).

In higher altitudes in China and the Himalayas In higher altitudes in China and the Himalayas ***Anastrophyllum assimile*** (Figure 5) occurs on both soil and rocks, including both acidic and calcareous rocks, on open rocky slopes below cliffs, in block screes and boulder fields, on cliffs, on mossy banks, and in wetter habitats including boulders by streams and wet rocks by waterfalls (Schill & Long 2003). In the forest it is usually mixed with other bryophytes and does not grow as an epiphyte. Schill and Long considered it to be tolerant of wetter substrates at high altitudes.

Adaptations

Schofield (1985) describes this species as one that can be quite large, growing in **tall turfs** of more or less erect shoots. These occur predominantly in open sites, forming **mats** of creeping shoots and firmly attached by rhizoids. Mägdefrau (1982) notes that these life forms have good capillary action that permits them to hold "considerable" amounts of water.

Figure 6. ***Takakia lepidozioides*** in wet habitat, a species that occurs in habitats similar to those of ***Anastrophyllum assimile*** along the shoreline of Takakia Lake on the Queen Charlotte Islands. Photo from Botany Website, UBC, with permission.

The leaf color is variable when the liverwort is moist, but when it is dry it is very dark brown, purplish brown, or blackish (Figure 5) (Schill & Long 2003). Herzog (1926) observed that liverworts with dark coloration usually occur in open habitats at higher altitudes where the light is very intense. The dark color is able to protect against these high light levels. In colder seasons, the dark pigments absorb more heat, maintaining a higher temperature in the mat. Capsules are unknown.

Anastrophyllum michauxii (Figure 7)

(syn. = *Sphenolobus michauxii*)

Distribution

Anastrophyllum michauxii (Figure 7) is widely distributed in the Holarctic region (Váňa 1996). It is a montane species that occurs in Europe (Austria, Bulgaria, France, the Czech Republic and Slovakia, Germany, Hungary, the former Yugoslavia, Italy, Romania, Poland, Finland, Sweden, Norway), in Asia (China, Japan), and in a few sites in North America (Dulin & Philippov 2012).

Figure 7. ***Anastrophyllum michauxii***, a Holarctic species that prefers rotten logs, especially near streams and other wet areas. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

On the Soyda River bank in the Russian Federation, Dulin and Philippov (2012) found ***Anastrophyllum michauxii*** (Figure 7) in the fern and herb spruce forest on a rotten spruce log. Choi *et al*. (2012) reported it as occurring near streams on Mt. Jiri-san in Korea. Nichols (1918) found it on wet rock cliffs on Cape Breton Island, Canada. Despite its occasional associations with water, the species seems most commonly to appear on rotten wood (Schuster & Patterson 1957; Dulin & Philippov 2012; Sofronova 2014).

Barbilophozia barbata (Figure 8)

Distribution

Barbilophozia barbata (Figure 8) is widespread in the Northern Hemisphere, especially in the boreal and mountain regions (Düll 2004; Wagner 2009).

Aquatic and Wet Habitats

Wagner described it as a species of terrestrial peaty substrates over rock where it usually occurs with other mosses and liverworts. In the West Carpathians, Mamczarz (1970) found it in rock communities associated with streams near Lacko. Papp *et al*. (2006) reported it from the Iskur River, Bulgaria, and its main tributaries. Düll (2004) reported it from siliceous rocks in Sicily and Erzberger (2002) from Hungary. Cain and Fulford (1948) found it to be common on moist igneous rock cliffs and boulders in Ontario, Canada, where it was often associated with other species of moist habitats, including ***Scapania nemorea*** (Figure 9), ***Lepidozia reptans*** (Figure 9), and ***Ptilidium ciliare*** (Figure 10).

Figure 8. ***Barbilophozia barbata***, a widespread Northern Hemisphere leafy liverwort from boreal and mountain regions, mostly in terrestrial habitats, but sometimes associated with streams. Photo by Hermann Schachner, through Creative Commons.

But it can also be found in wetter habitats. Lee (1944) reported it from a collection near a "little pool" in the low, partially grass-covered, tundra-like valleys of Greenland. Yamada and Iwatsuki (2006) reported it from fine-grained soil along a stream on the western slope of Chamga Mt. in Sakhalin Province, Japan, at 1406 m asl. In mountainous regions and the tundra, ***Barbilophozia barbata*** (Figure 8, Figure 11-Figure 12) can have an important role in ground cover **coenosis** (community of living beings belonging to different species and associated by way of inter-species interdependence or mutualism such as a food chain) (Troeva *et al*. 2010).

Figure 9. ***Lepidozia reptans*** (**small, pinnate liverwort**) and ***Scapania nemorea*** (**several larger leafy branches in lower left quadrant**), species that may accompany ***Barbilophozia barbata***. Photo by Bernd Haynold, through Creative Commons.

Figure 10. ***Ptilidium ciliare***, a species that may accompany ***Barbilophozia barbata*** on moist igneous cliffs. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Barbilophozia barbata*** in a patch on a boulder (see arrow). Photo by Sture Hermansson, with online permission.

Reproduction

In their study of propagule banks in boreal old-growth spruce forest in SE Norway, Rydgren and Hestmark (1997) found it among the living vegetation and as propagules in the soil. However, they only achieved ~5% germination from the soil bank propagules. On the other hand, Ross-Davis and Frego (2004) found that the similarity between aerial propagules and the extant flora of bryophytes in New Brunswick, Canada, was greater than the similarity of the buried propagules with the extant flora.

Figure 12. ***Barbilophozia barbata*** ventral side showing rhizoids that help it adhere to rocks. Photo by Hermann Schachner, through Creative Commons.

Biochemistry

There have been a number of biochemical studies on this genus, particularly indicating sesquiterpenes (Anderson *et al*. 1973; König *et al*. 1994; Nagashima *et al*. 1996, 1999; Asakawa 2001). Despite these sesquiterpenes and other substances that can serve as antibiotics, Bidartondo and Duckett (2010) reported the presence of the **Basidiomycota** fungus ***Sebacina*** (Figure 13) in association with ***Barbilophozia barbata*** (Figure 8, Figure 11-Figure 12) collected from Switzerland and the UK.

Figure 13. ***Sebacina incrustans*** on moss, a genus known to occur in association with ***Barbilophozia barbata***. Photo through Creative Commons.

Barbilophozia sudetica (Figure 14-Figure 15)

(syn. = *Lophozia sudetica*)

Figure 14. ***Barbilophozia sudetica***, an arctomontane species sometimes found on wet cliffs and stream banks. Photo by Hugues Tinguy, with permission.

Distribution

Barbilophozia sudetica (Figure 14-Figure 15). ***Barbilophozia sudetica*** is an **arctomontane** (occurring in Arctic habitats and mountain habitats farther south) species that is common in the northern Holarctic, but distribution extends to mountain ranges in East Asia, Spain, and Portugal and even to subtropical islands in Madeira at 32ºN (Bakalin 2004). In North America, Rahill (2018) found it among the tundra vegetation on Mount Washington, NH, USA.

Figure 15. ***Barbilophozia sudetica*** showing a color variant. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Konstantinova *et al*. (2002) found this species on a wet cliff and soil banks of a small creek of the Upper Bureya River in the Russian Far East. In Iceland, this species occurs on lava fields where the temperature does not exceed 39ºC (Buda *et al*. 2018). In the Aleutian Islands, Alaska, USA, the species is common, forming dark strands overgrowing the tundra ***Sphagnum*** (like Figure 78) and ***Sphagnum*** at the edge of a pond (Talbot *et al*. 2018). It also occurs on the bank of a streamlet, on the slope of a late snow area, on an outcrop face with ***Pohlia*** (Figure 16), in an alpine fellfield, on a old pier, and on damp humus on a cliff shelf.

Figure 16. ***Pohlia wahlenbergii*** with water beads, in a habitat suitable for ***Barbilophozia sudetica***. Photo by Michael Lüth, with permission.

Fungal Interactions

Like ***Barbilophozia barbata*** (Figure 8, Figure 11-Figure 12), ***B. sudetica*** (Figure 14-Figure 15) is known to form symbiotic mycorrhizal fungal associations (Wang & Qiu 2006) with the **Sebacinaceae** (Figure 13) (Kottke *et al*. 2003).

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22)

Distribution

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22) is distributed in Africa, Europe, northern and southern Asia, and North America (Alaska, Canada, USA) (ITIS 2020a).

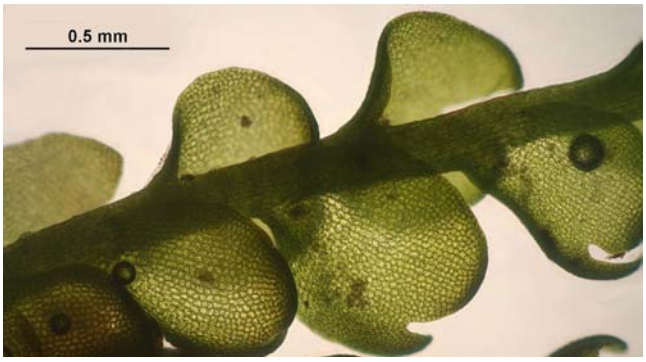

Figure 17. ***Gymnocolea inflata***, a species with widespread distribution that can occur in or out of water. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22) is a **hydroamphibiont** (living in transition zone between water and land, depending on water level; compare to euhydrobiont and geoamphibiont) (Figure 18), occurring in acid water (*p*H 3.5-4.2) in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). In Europe it often occurs with *Carex goodenoughii*, but is uncommon with ***Eleocharis quinqueflora*** (Figure 76) and ***Paludella squarrosa*** (Figure 19) (Geissler & Selldorf 1986). In streams of the Harz Mountains of Germany it occurs in the upstream reaches (Bley 1987). It also occurs in small lakes in southern Finland (Toivonen & Huttunen 1995).

Figure 18. ***Gymnocolea inflata*** growing in a wet habitat. Photo by Michael Lüth, with permission.

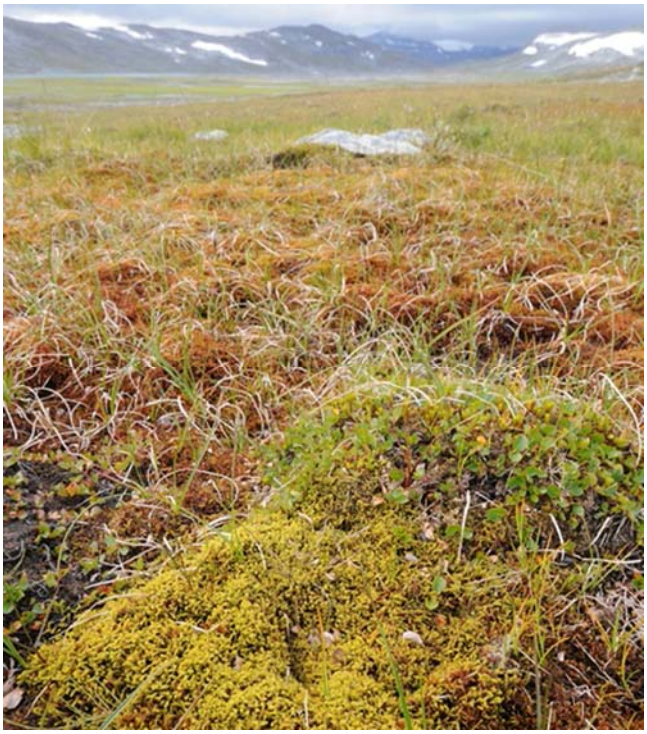

Figure 19. ***Paludella squarrosa*** habitat where ***Gymnocolea inflata*** avoids cohabiting with ***Paludella squarrosa*** and ***Eleocharis quinqueflora***. Photo by J. C. Schou, through Creative Commons.

In the Azores of Portugal, ***Gymnocolea inflata*** (Figure 20) occurs at 860-990 m asl (Schumacker & Gabriel 2002). Its habitat is permanently wet **pseudogley** (gley resulting from temporary or seasonal waterlogging due to poor drainage, rather than from permanent existence of high water table) soil overlain by a thin layer of **moor** (poor soil covered mainly with grass and heather; common in high latitudes and altitudes). The species is relatively common in wet heaths and bogs in Europe. Tyler *et al*. (1973) reported it from the ***Rhynchospora fusca*** (Figure 21) community where it covered the bottom of shallow depressions in heathland between bars.

Figure 20. ***Gymnocolea inflata*** showing one of its dark color forms. Photo by Michael Lüth, with permission.

Watson (1919) reported ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22) as form ***laxa*** on peaty sides of fast water streams, on banks with frequent submergence, and submerged in slow water with poor mineral salts.

Figure 21. ***Rhynchospora fusca***, a community that often has ***Gymnocolea inflata*** in heathland low areas. Photo by Peter M. Dziuk, with online permission for educational use.

In Westfalens, northwestern Germany, ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22) occurs between ***Sphagnum*** (Figure 22) (Koppe 1945). Tori *et al*. (1993) sampled peat profiles and found ***Gymnocolea inflata*** as part of the liverwort dominance with sparse ***Sphagnum*** cover. In the bare peat layer, only a few sedges occurred – no notable bryophytes. In Cataracts Provincial Park, Newfoundland, Canada, Weber (1976) found ***Gymnocolea inflata*** as a typical bog bryophyte, occupying open areas with a *p*H 3-4. Albinsson (1997) found that ***Gymnocolea inflata*** is among the liverworts that have narrow ecological amplitudes in mire habitats. Other smaller species tend to have wider amplitudes. Albinsson referred to those liverworts that required a habitat formed by other living bryophytes as using a **compromise strategy**. Those liverworts that prefer peat or litter as their substrate are included in the **avoidance strategy**. Albinsson found that those species that occur predominantly with ***Sphagnum*** (Figure 22) include those that are typically sterile, *i.e.*, not forming sexual reproductive structures. Frequently fertile species (*e.g.*, ***Cephalozia*** spp.; Figure 45-Figure 60) tend to occur on peat or litter, rather than on living ***Sphagnum***.

Figure 22. ***Gymnocolea inflata*** in Perrault Fen, Houghton Co., MI, USA, with ***Sphagnum***. Photo by Janice Glime.

Gough *et al*. (2006) found that ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22) colonized and covered **ferricrete**-cemented (hard, erosion-resistant layer of sedimentary rock, usually conglomerate or breccia, cemented together by iron oxides) silty alluvial sediments within seeps and streams in undisturbed, highly acidic, metal-rich habitats in east-central Alaska. These liverwort-covered sediments have high concentrations of metals, including Al, As, Cu, Fe, Hg, La, Mn, Pb, and Zn. The ***G. inflata*** thalli here are very small and compact, forming intimate associations with the iron-rich sediments of the seeps and streams. When the liverworts become covered by silt, the thalli grow upward, creating a dense fibrous ferricrete sediment below them. The dominance of ***G. inflata*** causes these areas to appear black. This species dominates both in very damp sites and in areas with flowing water.

Basile and Basile (1980) examined the effects of ammonium ions on form and hydroxyproline content of cell wall proteins in ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22). The presence of ammonium ions causes ventral leaves to develop, and the form of lateral leaves and branching pattern change due to a morphoregulatory role. This type of reaction might alter the appearance of this and other liverworts in the field as a result of the available nutrients.

Isopaches bicrenatus (Figure 23-Figure 24)

(syn. = *Lophozia bicrenata*)

Distribution

Isopaches bicrenatus ; Figure 23-Figure 24) is a widespread species in the temperate regions of the Northern Hemisphere (Gradstein *et al*. 2018). But it has appeared in a few widely separated areas, including southeastern Brazil, New Zealand, high elevations (>4000 m asl) in the Andes, Colombia (Gradstein *et al*. 2018), and the Dominican Republic in Central America (Bakalin 2008).

Figure 23. ***Isopaches bicrenatus***, a widespread species in temperate regions where it can occur on river banks, but is often on wood or in wet depressions. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

The habitat of this species includes earthy and gravelly substrates on river banks in the Haute Ardenne rivers of Belgium (Leclercq 1977). It is predominantly a terrestrial liverwort, often in association with other leafy liverworts, often on wood, but can also occur on wet soil in hollows or inundated shrublet-moss spruce forest, making pure patches or occurring with other liverworts (Dulin 2014).

Reproduction

Fulford (1955) described development of ***Isopaches bicrenatus*** (Figure 23-Figure 24). Like the typical liverworts, the spore germinates to produce a thalloid protonema. But under adverse conditions, it can produce a filamentous protonema instead, a phenomenon that has been observed in a number of liverworts. The mature plants produce a number of reddish gemmae (Figure 24) in clusters. These, and leaf fragments that regenerate easily, make reproduction and spread easy for this species.

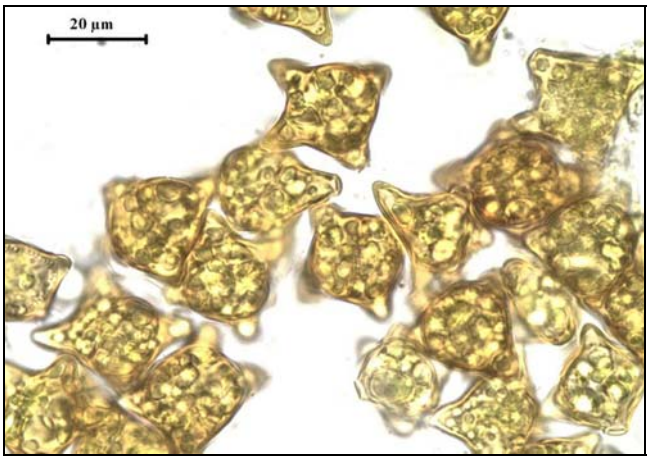

Figure 24. ***Isopaches bicrenatus*** gemmae; these become reddish at maturity. Photo by Hugues Tinguy, with permission.

Rivulariella gemmipara (Figure 25)

(syn. = *Chiloscyphus gemmiparus*)

Rivulariella gemmipara (Figure 25) seems to be a liverwort without a home – or with many homes. Whereas Wagner (2013) moved it from ***Chiloscyphus*** in the **Lophocoleaceae** to ***Rivulariella*** in the **Jungermanniaceae**, Patzak *et al*. (2016) consider its alignment to be with the **Scapaniaceae** *s.l.* Stotler and Crandall-Stotler (2017) argue for its placement in the **Anastrophyllaceae**, a family formerly included within the **Scapaniaceae**.

Distribution

Rivulariella gemmipara (Figure 25) is a subalpine or alpine species that is endemic to western North America (Wagner 2013). It is a species of concern, with only six known locations, those in Alaska, Oregon, California, and Utah, all in the USA.

Figure 25. ***Rivulariella gemmipara*** leaves from upward-growing stem. Photo courtesy of David Wagner.

Aquatic and Wet Habitats

Rivulariella gemmipara (Figure 25) grows in moderately fast water where there are small rocks (small pebbles to fist-sized cobbles) and gravel (Figure 26-Figure 31), avoiding areas with organic debris or muck over the substrate (Wagner 2013). It also avoids areas where the water surface is smooth or where the flow is very rapid. The suitable areas are typically permanent springs that keep the streambed submerged at all times, and that are exposed to sun most of the day, but that seldom have rapid flow due to any runoff. Rocks are its only known substrate. It is often associated with ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 27), ***Chiloscyphus polyanthos*** (Figure 28), and ***Scapania undulata*** (Figure 29).

Figure 26. ***Rivulariella gemmipara*** habitat in springfed stream. Photo courtesy of David Wagner.

Adaptations

Rivulariella gemmipara (Figure 25) lacks rhizoids in adults, but these are produced in germinating gemmae (Evans 1928). Perhaps this is enough to enable attachment, but it is an unusual characteristic for a bryophyte that grows on rocks in flowing water. Its slightly flattened stems are more in line with its habitat.

The species has horizontal, flattened stems (Figure 30) and upright, leafy stems (Wagner 2013). These flattened stems adhere closely to the substrate and lack rhizoids (David Wagner, pers. comm. 3 June 2020). The erect shoots differ distinctly from these pioneering horizontal stems. The latter lack underleaves, but the upright stems produce them, these eventually being as large as the lateral shoot leaves and transversely inserted. When the stone gets overturned, as it does sporadically, the upright leafy stems die and disappear, probably due to abrasion or decomposition, but the flat stems remain tightly adhered to the rocks, leaving blackish tracks (Figure 30, Figure 32). This method of gluing to the substrate seems to be a unique adaptation of this species.

Figure 27. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** from a wet habitat. Photo by Des Callaghan, with permission.

Figure 28. ***Chiloscyphus polyanthos***, a frequent species in siliceous mountain brooks where ***Jungermannia atrovirens*** is able to grow. Photo by Hermann Schachner, through Creative Commons.

Figure 29. ***Scapania undulata***, a species that associates with ***Marsupella aquatica*** on rocks in Maine, USA. Photo by Jan-Peter Frahm, with permission.

Figure 30. ***Rivulariella gemmipara*** flat horizontal stems on rock that was overturned. Photo courtesy of David Wagner.

Figure 31. ***Rivulariella gemmipara*** on pebbles in springfed stream. Photo courtesy of David Wagner.

Reproduction

Rivulariella gemmipara (Figure 25) is **monoicous**, thus facilitating sexual reproduction (Wagner 2013). It has marginal gemmae (Figure 33) on its leaves and these develop rhizoids as they germinate.

Figure 32. ***Rivulariella gemmipara*** on rock showing the upright plants on one side and the tracks of stems on a side that has been buried. Photo courtesy of David Wagner.

Figure 33. ***Rivulariella gemmipara*** leaf with gemmae. Photo courtesy of David Wagner.

Schljakovia kunzeana (Figure 34)

(syn. = *Lophozia kunzeana*, *Orthocaulis kunzeanus*)

Distribution

Schljakovia kunzeana (Figure 34) is widespread as an Arctic-alpine, circumboreal tundra species. It extends southward into the coniferous forest of the Great Lakes and alpine areas of Europe (Schuster 1969).

Figure 34. ***Schljakovia kunzeana*** is a widespread circumboreal species that can be found on some river banks and other wet habitats. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) described ***Schljakovia kunzeana*** (Figure 34) as a liverwort of alpine wet ground associated with fast water. Konstantinova *et al*. (2002) reported it from a boggy valley of a small creek of Upper Bureya River in the Russian Far East. In the Komi Republic of northwestern Russia, it occurs with other leafy liverworts on soil among sedges along the bank of the Ugum River (Dulin 2014). In the Russian Arctic National Park, Fedosov *et al*. (2018) reported that it occurs in willow and moss-dominated communities on smooth terraces, typically accompanied by other leafy liverworts.

Sphenolobus minutus (Figure 35, Figure 38-Figure 41)

(syn. = *Anastrophyllum minutum*)

Distribution

Sphenolobus minutus (Figure 35, Figure 38-Figure 41) is widely distributed in the Holarctic region (Schuster 1969), as well as Madagascar, Mexico, and the Russian Federation (TROPICOS 2020). Other reported locations include Norway, Czech Republic, Nova Scotia, Gaspé Peninsula, and Yukon in Canada, and Japan (Consortium of North American Bryophyte Herbarium 2020).

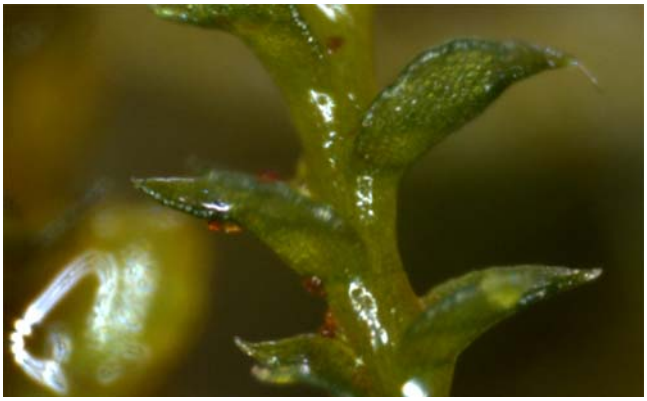

Figure 35. ***Sphenolobus minutus***, a widely distributed Holarctic liverwort that is less common further south except on the mountains; it lives on peaty soil and areas of high moisture, but can become submerged in montane streams. Photo by Jouko Rikkinen, through Creative Commons.

Aquatic and Wet Habitats

In western Canada ***Sphenolobus minutus*** (Figure 35, Figure 38-Figure 41) occurs submerged as a hemicalciphilous species in montane streams and on stream banks (Figure 36) (Vitt *et al*. 1986; Glime & Vitt 1987). In these habitats, it forms mats (Figure 38). It is especially common on peaty soil, but it can also occur on north-facing cliffs where there is little or no seepage but high atmospheric moisture (Schuster 1969). In the flume (Figure 37) at Franconia Notch, New Hampshire, USA it occurred on the flume wall (Glime 1982).

Figure 36. Calcareous stream in BC, Canada, where one might find ***Sphenolobus minutus***. Photo by Janice Glime.

Figure 37. Flume, Franconia Notch, NH, site where one can find ***Sphenolobus minutus*** on the walls. Photo by Janice Glime.

Figure 38. ***Sphenolobus minutus*** forming a mat. Photo by Jouko Rikkinen, through Creative Commons.

Reproduction

Like most of the leafy liverworts, ***Sphenolobus minutus*** (Figure 38) produces gemmae (Figure 39-Figure 41). These provide a means of surviving unfavorable conditions as well as dispersal.

Figure 39. ***Sphenolobus minutus*** with gemmae. Photo by Jouko Rikkinen, through Creative Commons.

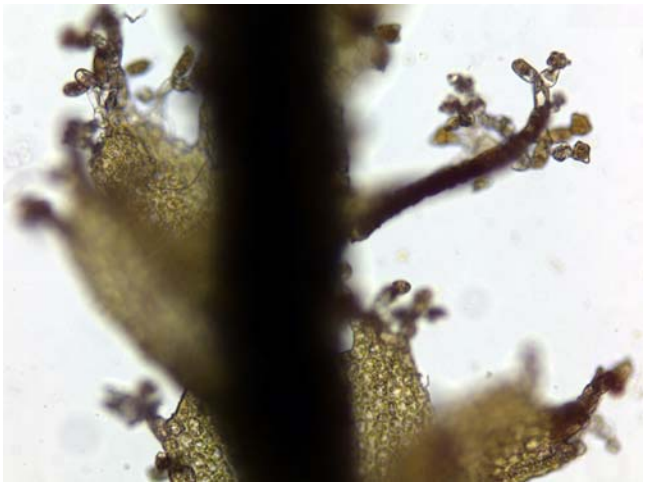

Figure 40. ***Sphenolobus minutus*** with gemmae on leaf tips. Photo by Jouko Rikkinen, through Creative Commons.

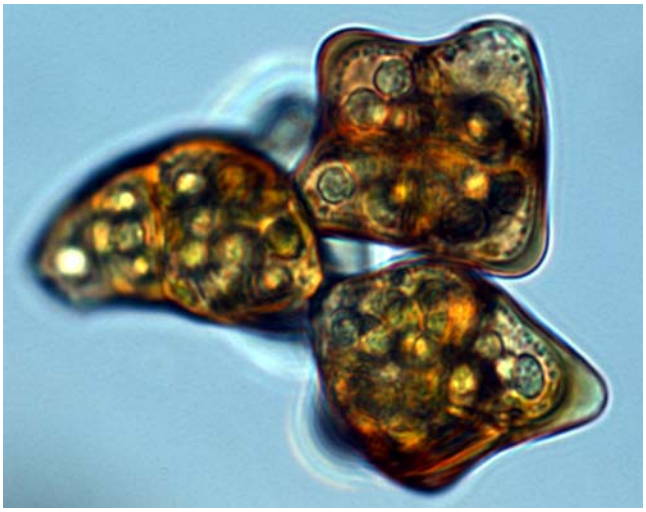

Figure 41. ***Sphenolobus minutus*** gemmae, showing their angular construction. Photo by Jouko Rikkinen, through Creative Commons.

Role

Kitagawa (1974) reported nematode galls (Figure 43-Figure 42) on ***Sphenolobus minutus*** (Figure 35, Figure 38-Figure 41) from Nepal. But other more common interactions seem to be lacking. For example, in their study on mycorrhizae in liverworts, Wang and Qiu (2006) could find no records of mycorrhizae for this species.

Figure 42. Nematode similar to the ones that can form galls on ***Sphenolobus minutus***. Photo by courtesy of Andi Cairns.

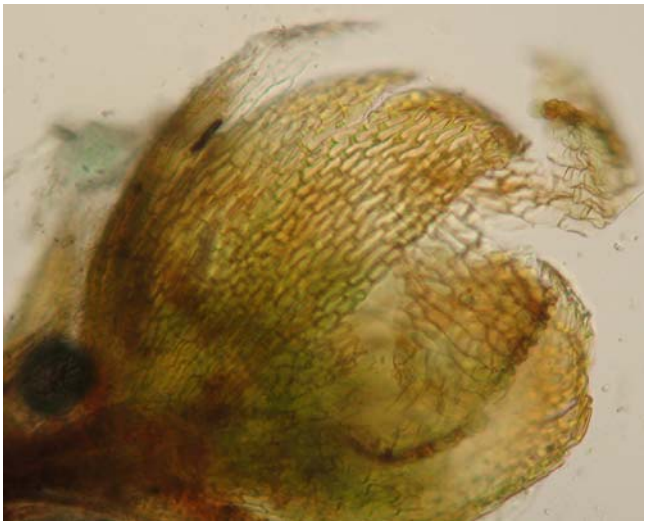

Figure 43. ***Bryum argenteum*** nematode galls, a parasitic attack that also occurs in ***Sphenolobus minutus***. Photo courtesy of Claudio Delgadillo Moya.

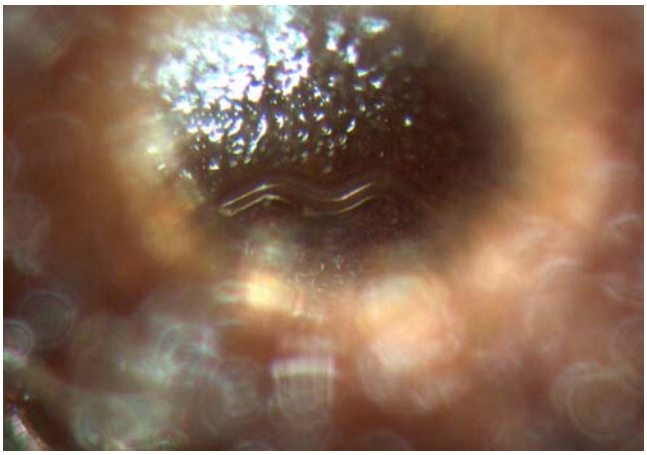

Figure 44. ***Buxbaumia aphylla*** nematode in gall showing nematode. Photo by Misha Ignatov, with permission.

Tetralophozia filiformis

(syn. = *Chandonanthus filiformis*, *Chandonanthus pusillus*)

Distribution

Tetralophozia filiformis has a very disjunctive distribution in Asia, Europe, and North America (Urmi 1983, 2015). Because its collections are widely separated (Japan, Himalayas, and Canada) and more recently in Russia (Konstantinova 2002b), it was originally treated as several species that have since been combined (Laine 1970).

Aquatic and Wet Habitats

In the Cantabrian Mountains of Spain it occurs on sheltered siliceous rocks with oceanic conditions (Urmi 1983). The records seem to be rather limited, but at least one record indicates that it occupies a dripping cliff near a waterfall of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002).

Cephaloziaceae

Cephalozia (Figure 45-Figure 59)

Cephalozia (Figure 45-Figure 59) occurs in small ponds of coastal barrens, Cape Breton Island, Canada (Nichols 1918). Albinsson (1997) found that ***Cephalozia*** species tended to have wider ecological amplitudes in Swedish mires than did the larger liverworts. The ***Cephalozia*** species are frequently fertile and seem to prefer peat and litter rather than living ***Sphagnum*** (like Figure 78) as a substrate, using an **avoidance strategy**.

Cephalozia ambigua (Figure 45-Figure 46)

Distribution

Cephalozia ambigua (Figure 45-Figure 46) is listed for China and Russia in TROPICOS (TROPICOS 2020). Geissler (1976) reported it from the Swiss Alps. Lorenz (1915) listed it for Scandinavia and Ellesmere Island in the Arctic Archipelago. Potemkin and Sofronova (2013) considered ***Cephalozia ambigua*** to be circumpolar, occurring in Arctic, alpine, and subalpine areas. In Europe it extends southward to the French Pyrenees, Spain, and Bulgaria. It extends from southern Polar Deserts to northern Taiga, mountain tundras, and elfin wood areas in the Far East.

Figure 45. ***Cephalozia bicuspidata*** complex; ***C. ambigua*** is a species from China and Russia and high elevations elsewhere in the Northern Hemisphere where it can occur on wet cliffs and lakeshore rocks or peaty soil. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

In the Swiss Alps, ***Cephalozia ambigua*** (Figure 45-Figure 46) occurs in alpine streams (Geissler 1976). In the Upper Bureya River of the Russian Far East, the species occurs on wet cliffs and rocks at the lake shore, often accompanied by other leafy liverworts (Konstantinova *et al*. 2002). It occurs on acid to neutral soil (incl. peaty soil and soil over the rocks) (Potemkin & Sofronova 2013).

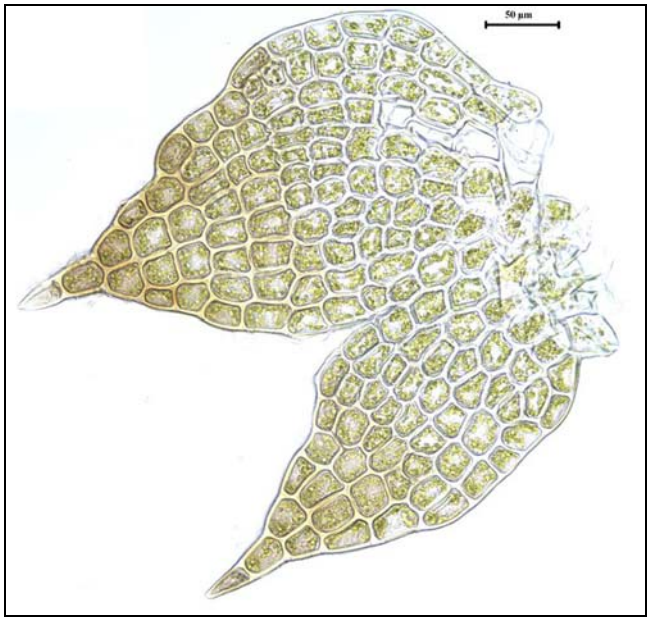

Figure 46. Leaf from ***Cephalozia bicuspidata*** complex. Note the thickened walls of the terminal cells compared to those at the base. Photo by Hugues Tinguy, with permission.

Adaptations

Potemkin and Sofronova (2013) noted that most species of ***Cephalozia*** never develop any secondary pigmentation, thus always occurring as green or whitish green (Figure 45). However, members of the ***Cephalozia bicuspidata*** complex [***C. ambigua*** (Figure 45-Figure 46), ***C. bicuspidata*** (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60), ***C. hamatiloba*** (Figure 48)] from sunlit habitats are typically brown and/or purple. Furthermore, ***C. catenulata*** (Figure 49), ***C. macrostachya*** (Figure 50), ***C. loitlesbergeri*** (Figure 51) and ***Nowellia curvifolia*** (syn. = *Cephalozia curvifolia*; Figure 52) often develop brown pigmentation.

Figure 47. ***Cephalozia bicuspidata*** exhibiting reddish-brown color from exposure to direct sunlight. Photo by Hermann Schachner, through Creative Commons.

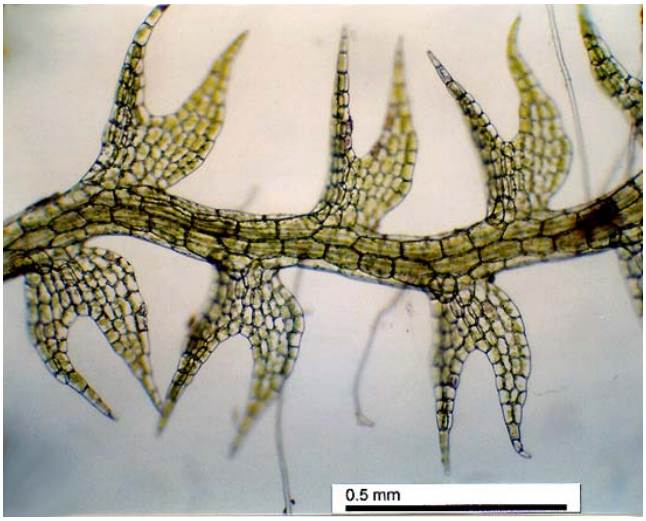

Figure 48. ***Cephalozia hamatiloba***, from the ***C. bicuspidata*** complex, is usually brown or purple in sunlit habitats. Photo by David H. Wagner, with permission.

Figure 49. ***Cephalozia catenulata***, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.

Figure 50. ***Cephalozia macrostachya***, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.

Figure 51. ***Cephalozia loitlesbergeri***, a species that can develop brown pigmentation in direct sunlight. Photo by Des Callaghan, with permission.

Figure 52. ***Nowellia curvifolia***, formerly in the genus ***Cephalozia***, red form from sunlit area. Photo by Hugues Tinguy, with permission.

Potemkin and Sofronova (2013) found that in ***Cephalozia ambigua*** (Figure 45-Figure 46) the extra thickenings of the apical wall of the terminal cells (Figure 46) is flexible, with the thickenings usually absent on soil, but present in populations growing on logs where humidity conditions are intermittent.

Cephalozia bicuspidata (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60)

Distribution

Cephalozia bicuspidata (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60) has a widespread distribution in the Northern Hemisphere, with scattered reports from South America and Africa (DiscoverLife 2020a). ***Cephalozia bicuspidata*** occurs mostly in northern and temperate Eurasia (not known in Asia south of Taiwan), Azores, North America, northern South America, Macaronesia, Africa (central African mountains, South Africa), and from remote islands of southern Indian (Reunion, Marion I., Crozet Is.) and Atlantic (Tristan da Cunha group) oceans, Chili, South Georgia, and Tasmania (Schuster 1974; Piippo 1990; Váňa 1993; Damsholt 2002).

Figure 53. ***Cephalozia bicuspidata***. Photo by Jay Avery, through Creative Commons.

Figure 54. ***Cephalozia bicuspidata*** on a wet log. Photo by Rambryo, through Creative Commons.

Aquatic and Wet Habitats

In his early summary of aquatic bryophytes, Watson (1919) described ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) as a species to be found on stream banks of streams with slow water and that provided frequent submergence. Light (1975) reported it from small lakes with low ion concentrations in Scottish mountains where ice cover lasted 4-7 months. Geissler (1976) found the species in alpine streams of the Swiss Alps. Similar habitats around Europe and North America support the species – earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium (Leclercq 1977); as calciphilous emergents of montane streams and streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987), contrasting with Schuster's (1953) statement of

intolerance of lime; upper and middle stream reaches in the Harz Mountains of Germany (Bley 1987); irrigation ditches (Beaucourt *et al*. 1987); in the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 55) of Thuringia, Germany (Marstaller 1987); in small lakes in southern Finland (Toivonen & Huttunen 1995); soil bank of a small creek of Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002); on the Southern Kuril Islands in the Goryachyee Lake area on fine-grained ground in crevices of a tufa cliff where they were splashed by water from the lake Bakalin 2007); in and along rivers (Ferreira *et al*. 2008). The most common sites for this species are sunny sites where the species uses decorticated rotting wood, rock, or bare mineral soil as substrate (Botany Website 2020).

Figure 55. ***Fontinalis antipyretica***, a species that, along with ***Platyhypnidium***, can be found in association with ***Cephalozia bicuspidata***. Photo by Michael Lüth, with permission.

Potemkin and Sofronova (2013) reported ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) on acid and occasionally more or less neutral substrata – bare soil, rocks, rotten wood (Figure 54), among mosses and among ***Sphagnum*** (like Figure 78), particularly, at bases of trees. Schuster (1953, p. 507) considered the ***C. bicuspidata*** complex to have no tolerance for even tiny amounts of lime.

One of the more unusual occurrences of ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) is in the Kootenay Paint Pots (Figure 57), British Columbia, Canada (Wehr & Whitton 1983). These are natural springs enriched with heavy metals and a *p*H range of 3.2-4.0. The springs have high levels of iron and zinc. These springs are home to 14 species of algae, but only one liverwort (***Cephalozia bicuspidata***) and one moss (***Dicranella heteromalla***; Figure 58). The latter occurred only as protonemata.

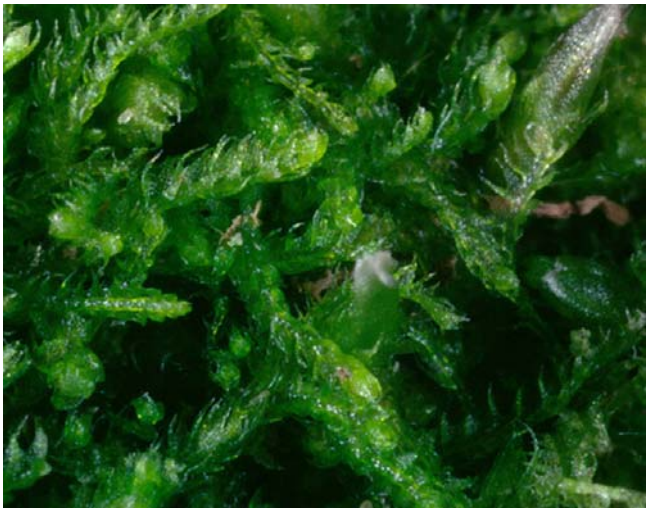

Figure 56. ***Cephalozia bicuspidata***, showing its mat growth form and a perianth in the upper right. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Figure 57. Kootenay National Park Paint Pots, where ***Cephalozia bicuspidata*** and ***Dicranella heteromalla*** are the only bryophytes able to grow in the iron-laden springs. Photo by Marek Ślusarczyk, through Creative Commons.

Figure 58. ***Dicranella heteromalla*** with young capsules, one of two bryophyte species able to grow at the Kootenay Paint Pots on the iron-rich mud. Photo by Janice Glime.

Adaptations

Potemkin and Sofronova (2013) observed that ***C. bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60), like ***C. ambigua*** (Figure 45-Figure 46), has flexible cell

wall thickenings (Figure 59) that seem to respond to intermittent humidity by developing stronger thickenings.

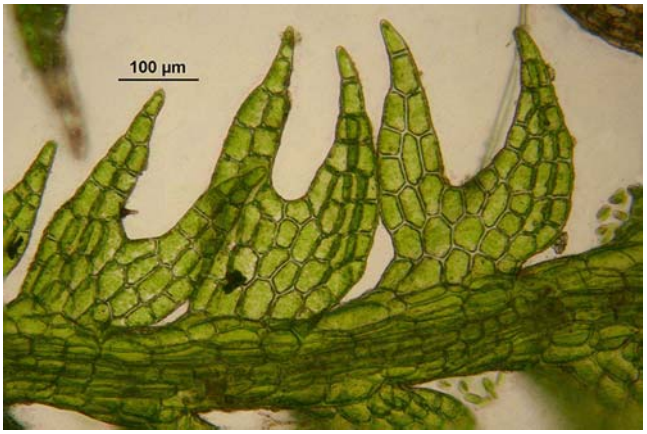

Figure 59. ***Cephalozia bicuspidata*** showing cell walls, in this case with no obvious thickening. Photo by Hermann Schachner through Creative Commons.

Proctor (1982) determined that the photosynthetic activity of the sporophytes of ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) is very low when compared with that of the gametophyte structures [perianth (Figure 60), bracts and uppermost leaves] associated with the sporophyte. In fact, the CO_2 uptake by the sporophyte is only a small percent of that translocated to it from the gametophyte. The greatest transport to the sporophyte seems to occur when the sporophyte has reached full size but is still green.

Figure 60. ***Cephalozia bicuspidata*** with numerous gametophyte perianths that dominate what you see. Photo by Michael Lüth, with permission.

The subspecies ***Cephalozia bicuspidata*** subsp. ***lammersiana*** (syn. = *Cephalozia lammersiana*, *Jungermannia lammerisiana*) occurs submerged in slow water with poor mineral salts (Watson 1919).

Role

At Tuckerman Ravine on Mt. Washington, New Hampshire, USA (1300 m asl), Duckett and Slack (2013) found ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59 on wet vertical rocks where it was associated with ***Scapania undulata*** (Figure 61), ***Solenostoma hyalinum*** (Figure 62), ***Blindia acuta*** (Figure 63), ***Philonotis fontana*** (Figure 64), ***Pohlia nutans*** (Figure 65), ***Racomitrium fasciculare*** (Figure 66), and ***R. heterosticum*** (Figure 67). ***Cephalozia bicuspidata*** on the mountain had no sexual reproductive structures, but they displayed extensive subterranean shoots that were leafless and contained fungi, most likely **Mucoromycotina**.

Figure 61. ***Scapania undulata*** (red with green edges) with the moss ***Philonotis fontana***, two species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by David T. Holyoak, with permission.

Figure 62. ***Solenostoma hyalinum*** with capsule, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Michael Lüth, with permission.

Figure 63. ***Blindia acuta***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by David Holyoak, with permission.

Figure 64. ***Philonotis fontana***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Janice Glime.

Figure 65. ***Pohlia nutans*** a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Michael Lüth, with permission.

Figure 66. ***Racomitrium fasciculare***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Janice Glime.

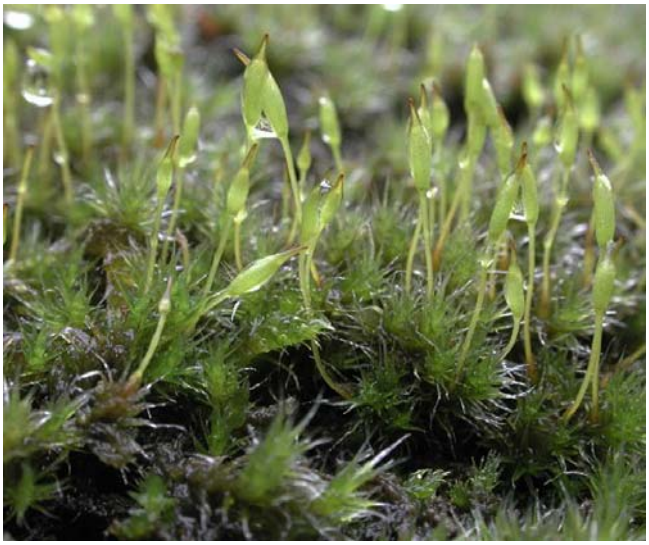

Figure 67. ***Racomitrium heterostichum***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Jan-Peter Frahm, with permission.

Reproduction

Duckett and Clymo (1988) found that many leafy liverworts regenerate from slabs cut from various depths of peat cores. They found that species that lack underground axes regenerate most abundantly at the surface, but not below 9 cm depth. Species like ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) that have such underground structures often have poor regeneration from the surface, but have much more regeneration down to 12 cm and even grow from samples down to 24-30 cm. This relationship proved to be true for both the cores from live ***Sphagnum***-covered surface (like Figure 78) and from the much older cut peat surface that had been recently colonized by liverworts. The researchers interpreted this to mean that most of the regeneration of ***C. bicuspidata*** is from underground axes rather than from spores or gemmae. The underground axes typically have a large biomass. All the axes had fungal associates that could be partially saprophytic or parasitic.

Fungal Interactions

Pressel and Duckett (2006) found that ***Mniaecia jungermanniae*** (Figure 68), a parasitic **Ascomycota**, associated with ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60). They hypothesized that the fungus could form a symbiotic relationship, producing swollen rhizoids on the liverwort. However, when cultured with ***Cephalozia bicuspidata***, the ***Mniaecia*** remained extracellular. Rather, it induced the formation of giant perichaetia that contained supernumerary archegonia followed by **parthenogenetic** (reproduction from egg without fertilization) and **apogamous** (reproduction in which sporophyte develops from gametophyte without fusion of gametes). They also observed similar giant perichaetia and abnormal perianths in the field.

Mniaecia jungermanniae (Figure 68) is known from 17 species of liverworts, including ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) as one of the most frequently inhabited liverwort species (Egertová *et al*. 2016). In the Czech Republic all the substrata of this liverwort were acidic and included soil, rocks, and boulders. The liverworts and their symbionts were typically located in the shade of both coniferous and broad-leafed forests. The fungus produces turquoise apothecia (Figure 68) on the liverworts (Duckett *et al*. 2004). In ***Cephalozia bicuspidata***, these occur on the shoots from January to March. This fungus does not colonize the rhizoids of ***C. bicuspidata***.

Figure 68. ***Mniaecia jungermanniae***, an **Ascomycota** fungus growing on ***Cephalozia bicuspidata***. Photo courtesy of Jan Gaisler.

Liepina (2012) reported the occurrence of fungal structures in the cell walls of ***Cephalozia bicuspidata*** (Figure 59) from a swamp. Kowal *et al*. (2018) noted that the rhizoids of leafy liverworts are often colonized by the **Ascomycota** fungus ***Pezoloma ericae*** (see Figure 69), forming associations that might carry out the same functions as mycorrhizae from members of the heath family **Ericaceae** in which there is bi-directional phosphorus for carbon exchange. These researchers measured exchanges of P and CO_2 in the liverwort-fungal association using tracers. They demonstrated the transfer of P from the fungus to the liverwort and transfer of carbon fixed by the liverwort to the fungus. The mycorrhizal liverworts also exhibited increased growth compared to those with no fungal partner.

Figure 69. ***Pezoloma ciliifera***; ***Pezoloma ericae*** occurs on ***Cephalozia bicuspidata***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Hasselbring (1911) provided an early report of fungi in the rhizoids of liverworts. When the fungal hypha makes contact with the rhizoid, a thickening appears on the inside of the opposite wall. As the hypha grows into the cell, cellulose is deposited ahead of the growing point, surrounding the hypha with a sheath of cellulose. Hasselbring isolated ***Mucor rhizophilus*** (Figure 70) in the **Zygomycota** from nine liverwort species and successfully cultured it with ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22), ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60), ***Cephaloziella*** sp. (Figure 100-Figure 105), and ***Lophozia ventricosa*** (Figure 112-Figure 116). This association appears to be neither mycorrhizal nor parasitic, although when the liverworts become strongly infected the plants experience an unfavorable reaction.

Figure 70. ***Mucor mucedo***; ***Mucor rhizophilus*** is known from nine liverwort species, including ***Gymnocolea inflata***. Photo by Lena Wild, through Creative Commons.

Fuscocephaloziopsis albescens (Figure 71-Figure 72)

(syn. = *Pleurocladula albescens*)

Distribution

Fuscocephaloziopsis albescens (Figure 71-Figure 72) is reported by GBIF (2020b) from Canada, USA, Iceland, Greenland, Russian Federation, Norway, Sweden, Switzerland, UK, and Japan. The species is also known from the Tatra Mountains of Poland and Slovakia (Górski 2015, 2016).

Figure 71. ***Fuscocephaloziopsis albescens***, a mostly Arctic and alpine species from Europe and North America, plus Japan, a species occasionally found in mires, seepage streamlets, and snowbeds. Photo by Des Callaghan, through Creative Commons.

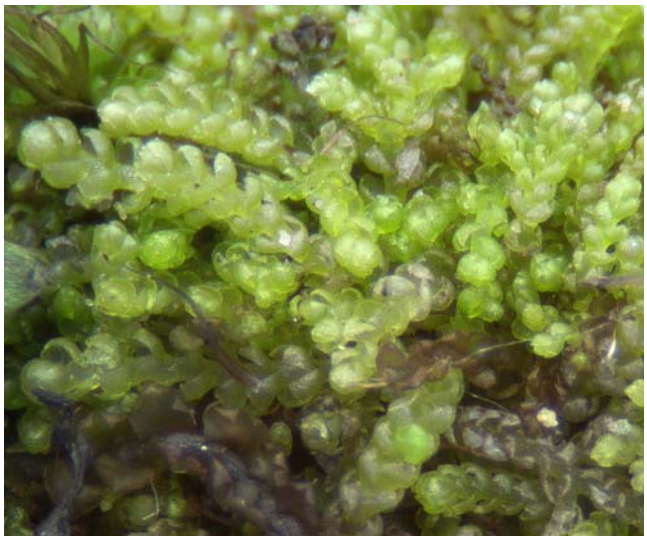

Figure 72. ***Fuscocephaloziopsis albescens*** forming a mat. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

This is not a frequent wetland species. Konstantinova *et al*. (2002) reported it from wet rocks of the Upper Bureya River in the Russian Far East. Górski (2015) reports it from snowbeds in the Tatra Mountains of Poland and Slovakia. There it occurred in an association with ***Pohlia nutans*** (Figure 65) (Górski 2016). Talbot *et al*. (2018) found it on Attu Island of the Aleutian Islands, again rare, on rock cliff outcrops, late snowbeds, cliff crevices, mesic mires, and seepage streamlets. It was sometimes mixed with other leafy liverworts.

Fuscocephaloziopsis connivens (Figure 73-Figure 78)

(syn. = *Cephalozia connivens*)

Distribution

Fuscocephaloziopsis connivens (Figure 73-Figure 78) is a Holarctic species, mostly occurring in boreal and temperate areas with a more or less humid microclimate (Potemkin & Sofronova 2013). This distribution includes records from Africa, the Caribbean, Europe, northern Asia, Middle America, Alaska, Canada, continental USA, Mexico, Oceania, and South America, even occurring on the Hawaiian Islands (ITISb).

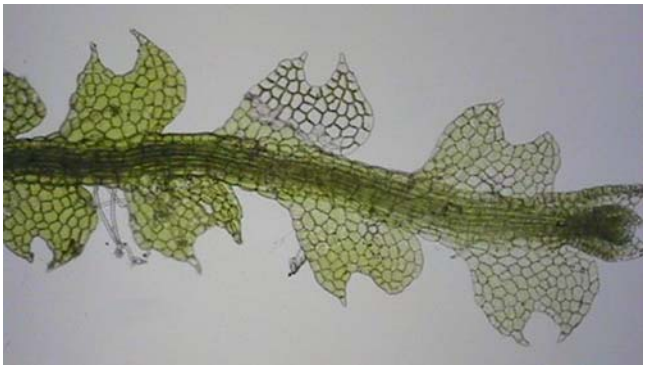

Figure 73. ***Fuscocephaloziopsis connivens***, a holarctic species on streambanks and in wetlands. Photo by Paul Davison, with permission

Figure 74. ***Fuscocephaloziopsis connivens***, the smaller liverwort mixed here with a larger liverwort. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Watson (1919) included this species in his list of aquatic and wetland species. It occurs on banks with frequent submergence and slow water (Figure 75). Geissler and Selldorf (1986) considered it to be uncommon in association with ***Eleocharis quinqueflora*** (Figure 76)**.** Henriques *et al*. (2017) considered ***Fuscocephaloziopsis connivens*** (Figure 73-Figure 78) to be a **humicolous** (thriving on humus) specialist.

Reproduction

Cores in peatlands demonstrate the regeneration capacity of ***Fuscocephaloziopsis connivens*** (Figure 77-Figure 78). Duckett and Clymo (1988) found it remarkable that this species was nearly absent at the surface where there were actively growing ***Sphagnum*** capitula (like Figure 78), but that it was able to regenerate from lower layers in the cores (3-12 cm depth). Nevertheless, Michael Lüth has photographed it growing well with ***Sphagnum*** (Figure 78).

Figure 75. ***Fuscocephaloziopsis connivens*** growing in a wetland habitat near water. Photo by Michael Lüth, with permission.

Figure 76. ***Eleocharis quinqueflora***, sometimes an associate of ***Fuscocephaloziopsis*** in alpine regions. Photo by Max Licher, through Creative Commons.

Figure 77. ***Fuscocephaloziopsis connivens*** with young capsule and perianth and demonstrating the light green leaf color. The spores have the potential to join the upper layers of peat in the spore bank. Photo by Des Callaghan, with permission.

Figure 78. ***Fuscocephaloziopsis connivens*** growing with ***Sphagnum*** and other bog/poor fen vegetation. Photo by Michael Lüth, with permission.

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82)

(syn. = *Cephalozia lunulifolia*, *Cephalozia media*)

Distribution

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) is widespread in the Northern Hemisphere (Hong 2007). TROPICOS specifically lists it for China, Japan, the Russian Federation, and the USA. Potemkin and Sofronova (2013) list it as a Holarctic boreal species, extending in the Eastern Hemisphere to Japan and SW China (Yunnan) but having a disjunct location in Cuba, as well as Guatemala (Gradstein & Váňa 1994).

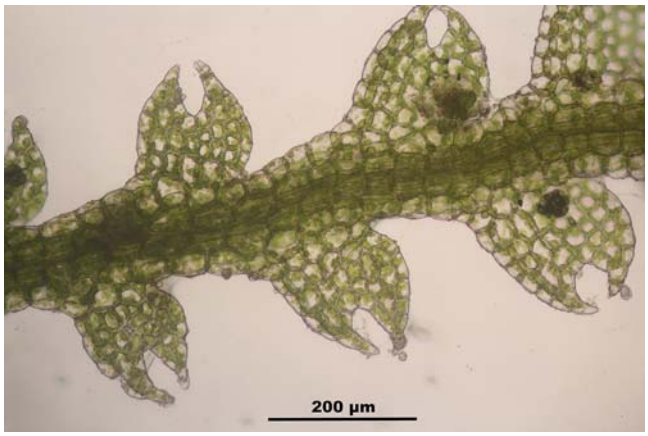

Figure 79. ***Fuscocephaloziopsis lunulifolia***, a widespread species in the Northern Hemisphere, occurring on rotten wood, soil, rocks, or among other mosses. It is associated with lakes, stream banks, and bare peat in subalpine zones and the taiga. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Potemkin and Sofronova (2013), from their experience in Russia, describe this species as one found among ***Sphagnum*** (like Figure 78), on rotten wood, more rare among other mosses, on humus soil, rocks, or fine sandy soil. The ***Fuscocephaloziopsis lunulifolia*** plants are medium-sized, whitish green, and lack secondary pigmentation (Figure 79, Figure 81).

Nichols (1918) reported this species from moist hollows between ***Sphagnum*** hummocks (Figure 80) on

Cape Breton Island, Canada. In the Altai Mountains of Russia, Váňa and Ignatov (1995) considered it rare in the upper taiga and subalpine zones, where it occurred on sides of hummocks, lake shores just above the water level, and on bare peat of bogs. In the Takakia Lake area of the Queen Charlotte Islands, western Canada, Hong (2007) found it on shaded decayed wood, wet rocks, and stream banks. Jonsson (1996) reported ***Fuscocephaloziopsis lunulifolia*** (Figure 79, Figure 81-Figure 82) from the riparian zone of the H. J. Andrews Experimental Forest in the western Cascades, Oregon, USA.

Figure 80. ***Sphagnum*** hummocks and hollows, similar to the ones where ***Fuscocephaloziopsis lunulifolia*** can occur. Photo by Nicholas A. Tonelli, through Creative Commons.

Figure 81. ***Fuscocephaloziopsis lunulifolia*** forming a mat on its substrate. Photo by Michael Lüth, with permission.

Adaptations

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) presents evenly thickened leaf cell walls (Figure 82) that are unable to develop extra thickenings in the apical wall of the terminal cells in **xylicolous** (living on wood that has lost its bark) habitats, making it less flexible in these adaptations compared to ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) (Potemkin & Sofronova 2013).

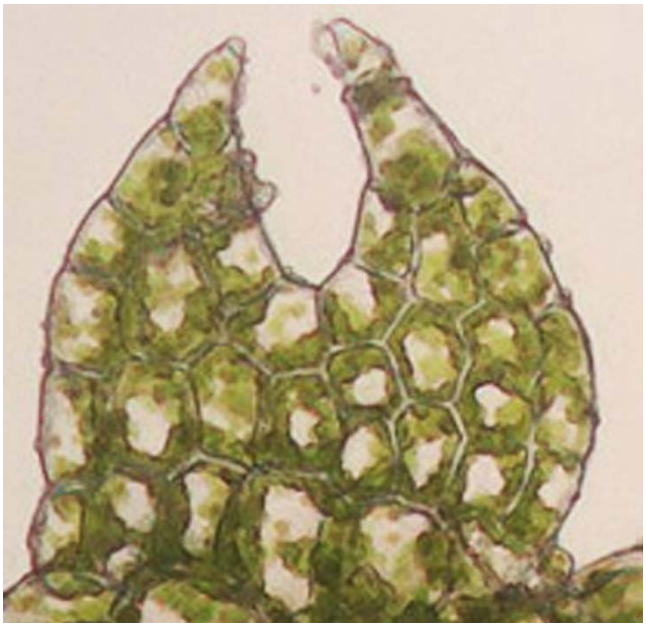

Figure 82. ***Fuscocephaloziopsis lunulifolia*** cells showing walls that are evenly thickened. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) can be dioicous or autoicous. The propagule bank seems to be rather inconsequential for this species. In their study in a boreal old-growth spruce forest in SE Norway, Rydgren and Hestmark (1997) observed germination in fewer than 5% of the samples. However, it likewise was poorly represented in the extant flora sampled, occurring in only 1 of 50 samples.

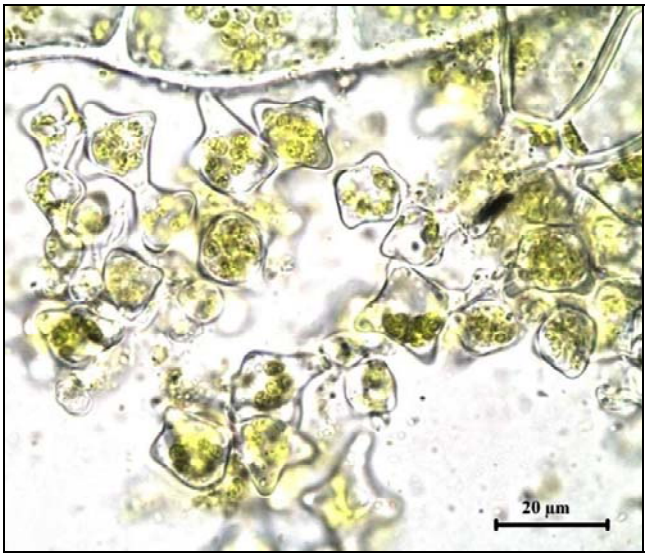

Figure 83. ***Fuscocephaloziopsis lunulifolia*** gemmae, potential members of the sporebank in upper layers of peat. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Wang and Qiu (2006) reported mycorrhizal relationships with ***Fuscocephaloziopsis lunulifolia*** (Figure 79, Figure 81-Figure 82).

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90)

(syn. = *Odontoschisma denudatum* subsp. *elongatum*)

Distribution

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90) presents a distribution in the Caribbean, Europe, Northern Asia, Alaska, Canada, and the continental USA (ITIS 2020c).

Figure 84. ***Odontoschisma elongatum***, a Northern Hemisphere species that can occur in mires. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

This species likewise is not a common member of wetland communities. Geissler and Selldorf (1986) found it with *Trichophorum cespitosum* (Figure 85) and *Carex chillanensis*, and uncommonly with *Eleocharis quinqueflora* (Figure 76) and ***Paludella squarrosa*** (Figure 19). Albinsson (1997) reported this species from ***Sphagnum*** associations (like Figure 78) in mires, noting that liverworts were encountered more often among species of ***Sphagnum*** in the subgenera ***Sphagnum*** (Figure 86) and ***Acutifolia*** (Figure 87) than in subgenus ***Cuspidata*** (Figure 88).

Figure 85. ***Trichophorum cespitosum***, a sedge species that sometimes contributes to making a suitable habitat for ***Odontoschisma elongatum***. Photo by Peter M. Dziuk, with online permission for educational use.

Figure 86. ***Sphagnum magellanicum***, a member of the subgenus ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 87. ***Sphagnum capillifolium***, a member of the subgenus ***Acutifolia***. Photo by Blanka Shaw, with permission.

Figure 88. ***Sphagnum tenellum***, a member of the subgenus ***Cuspidata***. Photo by David Holyoak, with permission.

Adaptations

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90) can be a bright green (Figure 89), but more commonly has a yellowish or brownish pigment (Figure

90) (Evans 1912). Even a deep blackish purple color is relatively common. Shoots initially produce branches very sparingly, producing unbranched ascending axes. As the stems become longer, they become prostrate and produce the typical intercalary branches, some lateral and some ventral. A few of these are flagelliform (Figure 89) and grow downward, holding the plant in place, especially in its ***Sphagnum*** habitat, and rhizoids are scarce.

Figure 89. ***Odontoschisma elongatum*** with flagelliform stolon (**arrow**) and green color. Photo by Norbert Schnyder, with permission.

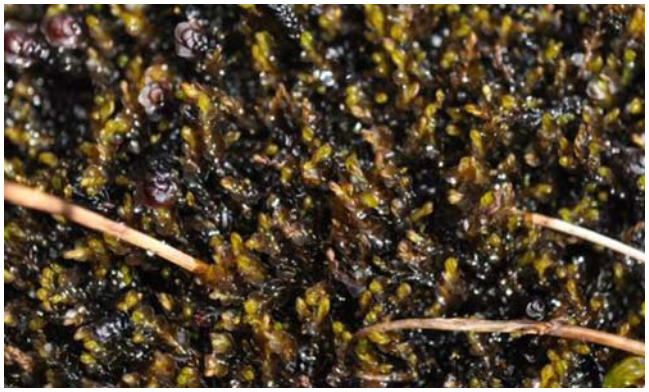

Figure 90. ***Odontoschisma elongatum*** from a wetland community, exhibiting brownish and golden coloration. Photo by Andrew Hodgson, with permission.

Role

Cyanobacteria (Figure 91) can be involved in symbiotic relationships with leafy liverworts (Rikkinen 2017). These can be important sources of fixed nitrogen that is available to the liverworts. Although Rikkinen investigated terrestrial populations, this relationship might as well occur in wetland species. In ***Odontoschisma elongatum*** (Figure 84, Figure 89-Figure 90) the slime papillae at the margins and surface of reduced underleaves near the growing tip were uninfected with any symbiont. But contrary to earlier observations, Rikkinen found that both bacteria and fungal hyphae could attach to the surface of the young slime papillae. The fungus would eventually infect the papilla with its haustoria. In later stages one can observe heavy fungal infections of the slime papillae, and these papillae are eventually shed from the plant.

Figure 91. ***Nostoc linckia***, a **Cyanobacterium**; some species of ***Nostoc*** are common on leafy liverworts as symbionts. Photo from Proyecto Agua, through Creative Commons.

Reproduction

The species is dioicous and male plants are apparently rare (Evans 1912). Despite the difficulty of sexual reproduction, gemmae are also rather rare. This suggests that fragments may be an important means of reproduction and spreading.

Fungal Interactions

Pocock and Duckett (1985) found no mycorrhizal fungi in ***Odontoschisma elongatum*** (Figure 84, Figure 89-Figure 90) among British liverworts. Likewise, Wang and Qiu (2006) found no records of mycorrhizae in ***Odontoschisma elongatum***. Nevertheless, Duckett *et al.* (1991) reported not only flagelliform branches, but also rhizoidal fungi from British ***O. elongatum***.

Odontoschisma fluitans (Figure 92-Figure 93)

(syn. = *Cephalozia fluitans*, *Cladopodiella fluitans*)

Distribution

Odontoschisma fluitans (Figure 92-Figure 93) is distributed in temperate regions of the northern hemisphere and occurs in Europe and eastern North America (Gradstein & Ilkiu-Borges 2015).

Figure 92. ***Odontoschisma fluitans***, a species of Northern Hemisphere temperate regions, known from stream banks, heathlands, peat bogs, and small lakes. Photo by Jean Faubert, with permission.

Aquatic and Wet Habitats

Few records seem to exist for this species in wetlands. Nevertheless, Watson (1919) included it in his treatment of aquatic and wetland species, attributing it to banks with frequent submergence and slow water (Figure 93). Koppe (1945) reported it from ***Sphagnum*** moors in Westfalens, northwestern Germany. It is typically associated with ***Sphagnum*** in heathlands and peat bogs (Gradstein & Ilkiu-Borges 2015). But Toivonen and Huttunen (1995) reported it from small lakes in southern Finland.

Figure 93. ***Odontoschisma fluitans*** forming mats. Photo by David T. Holyoak, with permission.

Reproduction

Unlike some members of the genus, ***Odontoschisma fluitans*** lacks gemmae (Figure 92-Figure 93) (Gradstein & Ilkiu-Borges 2015).

Odontoschisma sphagni (Figure 94-Figure 97, Figure 99)

(syn. = *Jungermannia sphagni*, *Odontoschisma prostratum*)

In North America, this species has been widely known as *Odontoschisma prostratum*, but based on molecular data, Gradstein and Ilkiu-Borges (2015) considered it to belong to the same species as the European ***O. sphagni*** (Figure 94-Figure 95). ***Odontoschisma sphagni*** is exceptional in the genus in being autoicous; other members are dioicous (Gradstein & Ilkiu-Borges 2015).

Figure 94. ***Odontoschisma sphagni***, a species that is both Holarctic and tropical, especially occurring in bogs and other peatlands. Note the whitish underground shoots. Photo by Des Callahan, with permission.

Figure 95. ***Odontoschisma sphagni.*** Photo by Michael Lüth, with permission.

Distribution

Odontoschisma sphagni (Figure 94-Figure 97, Figure 99) occurs in tropical America as well as the Holarctic region, including records from Europe, North America, Mexico, and the Greater Antilles (Gradstein & Ilkiu-Borges 2015).

Aquatic and Wet Habitats

Bley (1987) legitimizes ***Odontoschisma sphagni*** (Figure 94-Figure 97, Figure 99) as an aquatic species (Figure 96-Figure 97), reporting it from the upper reaches of streams in the Harz Mountains of Germany. Gradstein and Ilkiu-Borges (2015) summarize its habitats to include "raised bogs between ***Sphagnum***, on moist, often somewhat peaty soil, on rotten or dead wood, or on thin soil over moist sandstone rock in evergreen or deciduous forests. Sometimes the species grows over ***Leucobryum*** (Figure 98) or among other mosses" (Figure 99).

Figure 96. ***Odontoschisma sphagni*** well hydrated, showing its (mostly) green form. Photo by Michael Lüth, with permission.

Figure 97. ***Odontoschisma sphagni*** in a dry state, showing its reddish color form. Photo by Michael Lüth, with permission.

Figure 98. ***Leucobryum glaucum***; ***Odontoschisma sphagni*** will sometimes grow over members of this moss genus. Photo by Amadej Trnkoczy, through Creative Commons.

Figure 99. ***Odontoschisma sphagni***, growing here with the moss ***Polytrichum***. Photo by Michael Lüth, with permission.

Reproduction

Duckett and Clymo (1988) found that ***Odontoschisma sphagni*** (Figure 94-Figure 97, Figure 99) occurred in core samples from 12-23 cm depth, but was absent from the surface. Because this species does not produce gemmae, but exhibits the same regeneration patterns as species that do, Duckett and Clymo considered the regeneration of liverworts in these habitats not to be the result of gemmae. It is more likely that they are underground shoots (Figure 94). It is also possible that in ***Odontoschisma sphagni*** they result from spores because this species is **autoicous** (having male and female organs on same plant but on separate branches) (Gradstein & Ilkiu-Borges 2015).

Cephaloziellaceae

Cephaloziella (Figure 100-Figure 105)

Cephaloziella (Figure 100-Figure 105) is a widespread genus in a variety of habitats. In the maritime Antarctic, it forms bryophyte carpets in wet areas and depressions around melt pools and streams (Gimingham & Birse 1957). In southern Finland, it occurs in small lakes (Toivonen & Huttunen 1995).

Cephaloziella hampeana (Figure 100-Figure 101)

Distribution

Cephaloziella hampeana (Figure 100-Figure 101) has a scattered distribution that may include disjunct locations or just missing collection areas. When Flores *et al*. (2017) discovered it in Argentina, they raised the question of its disjunct distribution, noting the importance of high elevation locations for species like this. It is widely distributed in the Northern Hemisphere, with its most southern localities previously known from Vera Cruz in Mexico and El Quiche in Guatemala.

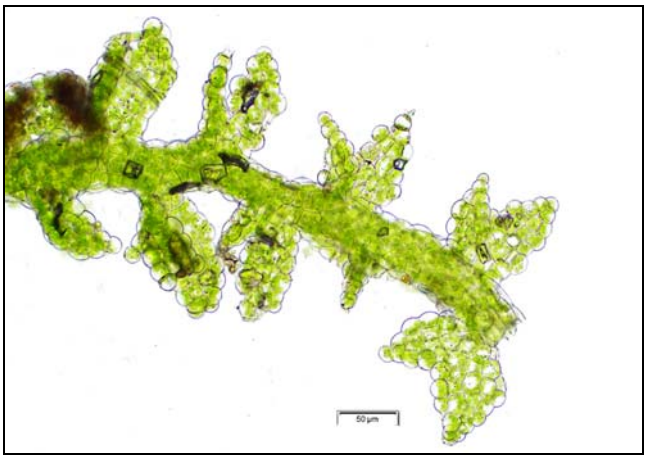

Figure 100. ***Cephaloziella hampeana***, a species widely distributed in the Northern Hemisphere, but also at high elevations in the Southern Hemisphere, where it can be found in fens and mires and similar wetlands. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Aquatic and Wet Habitats

Cephaloziella hampeana (Figure 100-Figure 101) appears to be mostly terrestrial, but its tolerance of moisture permits it to live in wetland habitats. Ingerpuu *et al*. (2014) report it from fens and mires in Estonia. In Argentina, as with a number of other Neotropical liverworts, ***C. hampeana*** occurs on soil, associated with

wetlands (Flores *et al*. 2017). In Tennessee, USA, at Abrams Falls Trails, it occurs on moist soil. In Connecticut, USA, the liverwort occupies crevices or the surface of drier cliffs in a ravine (Nichols 1916). In Turkey Run State Park, Indiana, USA, Ellis (1973) found ***Cephaloziella hampeana*** on moist ground on peat mosses, on the sides of ditches, and on sandy and turfy ground. Sass-Gyarmati *et al*. (2015) found ***Cephaloziella hampeana*** on one of the control plots in their experiments on temperature increase and drought. In that heathland vegetation, the species typically grows on acidic or neutral substrates, requiring a somewhat colder temperature range that might not be available as the climate warms, but it has a wide tolerance for moisture levels.

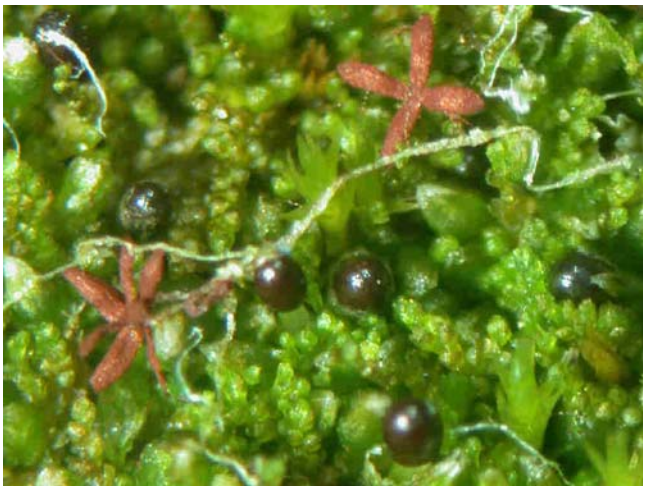

Figure 101. ***Cephaloziella hampeana*** with both gemmae and sporophytes. Photo by David T. Holyoak, with permission.

Fungal Interactions

As for many liverwort species, Wang and Qiu (2006) list it among the species that have fungal associations. The nature of this association needs to be explored.

Cephaloziella rubella (Figure 102-Figure 105)

Distribution

Cephaloziella rubella (Figure 102-Figure 105) occurs in the Northern Hemisphere, mostly in the Temperate Zone: Europe, Asia, North America (ITIS 2020d)

Figure 102. ***Cephaloziella rubella***, a species of the temperate Northern Hemisphere that occurs occasionally on montane stream banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

This species occurs as a submerged hemicalciphilous species in montane streams and on stream banks in western Canada (Figure 103) (Vitt *et al.* 1986; Glime & Vitt 1987). But elsewhere, reports of its wetland presence are rare. Strout (1976) found it in Larks Lake, Michigan, USA, where it hosted an apparent symbiont in the **Cyanobacteria** (see Figure 91). In addition to its cyanobacterial symbiont, ***Cephaloziella rubella*** (Figure 102-Figure 105) has fungal associations (Wang & Qiu 2006).

Figure 103. Glacial melt stream where ***Cephaloziella rubella*** grows in BC, Canada. Photo by Janice Glime.

Figure 104. ***Cephaloziella rubella*** showing its growth pattern in mats. Photo by Michael Lüth, with permission.

Figure 105. ***Cephaloziella rubella*** showing the large, dense mats it can form. Photo by Michael Lüth, with permission.

Kymatocalyx (Figure 106-Figure 111)

(syn. = *Ruttnerella*, *Stenorrhipis*)

Kymatocalyx (Figure 106-Figure 111) is a leafy liverwort known from Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011). This is a pantropical rheophytic genus that grows in or near running water, on periodically submersed rocks, in waterfalls, on wet cliffs, and similarly wet habitats. Members of this genus produce very small erect leafy shoots from creeping, stoloniform axes.

Kymatocalyx africanus (Figure 106)

Distribution

Kymatocalyx africanus (Figure 106) occurs in the Uluguru Mts. (1600-2350 m asl) of Tanzania, and Mt. Mulanje (1200-2220 m asl), Malawi.

Figure 106. ***Kymatocalyx africanus***, a species of limited known distribution in eastern Africa where it can grow partially submerged in streams and wet places. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

The species occurs in montane forest areas on shady granitic rocks and boulders, on soil banks or on thin peat over rocks in streams or wet places, partially submerged in water (Gradstein & Váňa 1999). The type was found on Mt. Mulanje in the bed of a seasonal stream on thin gritty soil over a granite boulder at 1740 m asl.

Reproduction

Kymatocalyx africanus (Figure 106) is **cladautoicous** (having male sexual organs on special branch separate from female organs) (Gradstein & Váňa 1999).

Kymatocalyx cubensis (Figure 107)

In Madagascar, ***Kymatocalyx cubensis*** (Figure 107) can occur 0.3-1 m above the tidal surface, suggesting that it is salt-tolerant (Pócs 1998). Its only claim to being hydrophilic is its nearness to the ocean water.

Figure 107. ***Kymatocalyx cubensis***, a species that occurs within a meter of the tidal surface in Madagascar. Photo courtesy of Tamás Pócs.

Kymatocalyx dominicensis (Figure 108)

Distribution

Kymatocalyx dominicensis (Figure 108) is known from Cuba (1210 m asl), Puerto Rico (900 m asl), Dominica (800 m asl), St. Vincent Is., Guyana (150-1200 m asl), Venezuela (500 m asl), Colombia (1800 m asl), Bolivia (850 m asl), and Brazil (10-1850 m asl) in the Western Hemisphere and in Madagascar (1 m asl) in the Eastern Hemisphere (Gradstein & Váňa 1999).

Figure 108. ***Kymatocalyx dominicensis***, a species known from the Neotropics and Madagascar where it can occur on shaded rocks along rivers, in waterfalls, and at times be partly submerged. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

Like other taxa of the genus, ***Kymatocalyx dominicensis*** (Figure 108) grows on shaded rocks along rivers, in waterfalls, etc., often partly submerged, in moist tropical lowland and lower montane areas (Gradstein & Váňa 1999). It was very common as dark green mats on volcanic stones along the trail in Dominica (Gradstein 1989).

Kymatocalyx madagascariensis (Figure 109-Figure 110)

Distribution

Kymatocalyx madagascariensis (Figure 109-Figure 110) seems to be restricted to the East African islands: Madagascar (0.3-1380 m asl), Mauritius (700 m asl), Reunion (200-1800 m asl), and Comoro Archipelago (500-1580 m asl). Material from mainland Africa belongs to ***K. africanus*** (Figure 106) (Gradstein & Váňa 1999).

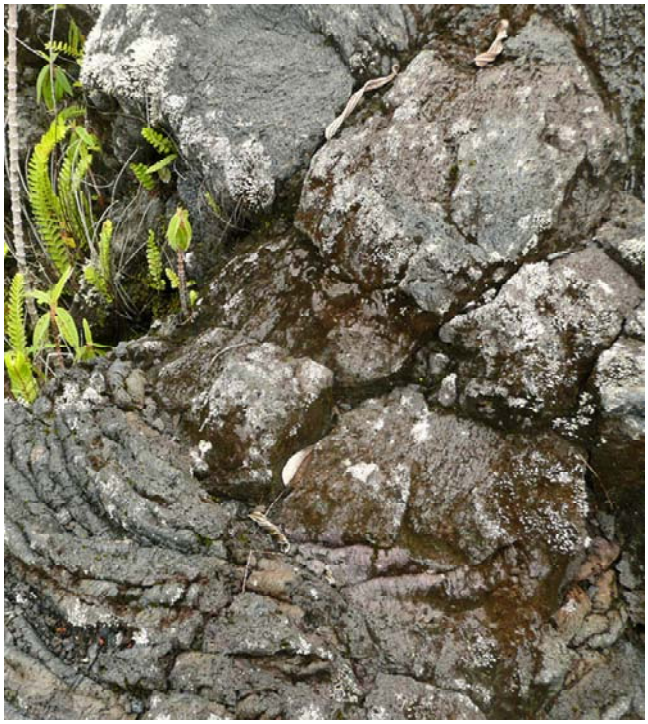

Figure 110. ***Kymatocalyx madagascariensis*** in crevices on old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.

Figure 109. ***Kymatocalyx madagascariensis***, a species endemic to east African islands, occupying lava rocks where they may be submerged at times of high rainfall. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

Kymatocalyx madagascariensis (Figure 109-Figure 110) grows on shaded granite and basaltic lava rocks, on cliffs and boulders near waterfalls, partly submerged or irrigated, in moist tropical lowland and montane rainforest areas (Gradstein & Váňa 1999). In Madagascar, Comores, and the Mascarenes it occurs mostly on volcanic rocks of temporary water flows (see Figure 111), but also occurs on wet soil on roadsides. On Réunion Island it occurs in shady cracks in 5-20-year-old lava flows (Figure 110) (Tamás Pócs, pers. comm. 3 March 2020).

Figure 111. ***Kymatocalyx madagascariensis*** temporary water flow habitat on old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.

Kymatocalyx rhizomatica

(syn. = *Ruttnerella rhizocaula*)

Distribution

Kymatocalyx rhizomatica was reported from tropical wet areas by Ruttner (1955). It is a pantropical species from Malaysia, Sarawak (300 m asl), Sumatra, Costa Rica (150-600 m asl), Panama (150-300 m asl), and Colombia (700 m asl) (Gradstein & Váňa 1999).

Aquatic and Wet Habitats

Kymatocalyx rhizomatica grows on volcanic rock, stones, or moist earth in and along rivulets, in waterfalls and on trails in lowland and submontane rainforest areas (Gradstein & Váňa 1999).

Reproduction

Kymatocalyx rhizomatica is cladautoicous and gemmae observations are rare (Gradstein & Váňa 1999).

Lophoziaceae

Lophozia (Figure 112-Figure 121)

In western Canada, Glime and Vitt (1987) considered members of ***Lophozia*** in their stream study to be a restricted terrestrial of montane streams and streambanks. These are not submersed species.

Lophozia ventricosa (Figure 112-Figure 116)

Distribution

Records of ***Lophozia ventricosa*** (Figure 112-Figure 116) are almost entirely restricted to the Northern Hemisphere, from the Arctic to the subtropics (DiscoverLife 2020b). It occurs in the Antarctic/Southern Ocean region on an island off the southern coast of Australia, Europe, Asia, and North America (Alaska, Canada, Continental USA) (ITIS 2020e).

Figure 112. ***Lophozia ventricosa*** occurs from the Arctic to the subtropics in the Northern Hemisphere. Its wet habitats include being submerged in small lakes, on river banks, and in fens. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Lophozia ventricosa (Figure 112-Figure 116) can be truly aquatic in small lakes in the Scottish mountains where the ice cover lasts 4-7 months and the water is low in ions (Light 1975). In Belgium, Leclercq (1977) reported it on earthy and gravelly substrates of river banks (Figure 113) in the Haute Ardenne rivers. Lenz (2011) reported this species from fens in the Bighorn National Forest, Wyoming, USA.

Figure 113. ***Lophozia ventricosa***, appearing here with other bryophytes on a gravelly substrate. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Lophozia ventricosa (Figure 112-Figure 116) produces gemmiferous shoots (Figure 114-Figure 116). Algar-Hedderson *et al*. (2013) found little difference in the gemma production between a boreal population in central Norway and one in the Arctic tundra on Svalbard. There was a significant difference in that shoots in the boreal site tended to produce somewhat more gemmae and form larger, denser colonies. This combination results in a somewhat higher colony level output in the boreal site.

Figure 114. ***Lophozia ventricosa*** with gemmiferous branches. Photo by Jan-Peter Frahm, with permission.

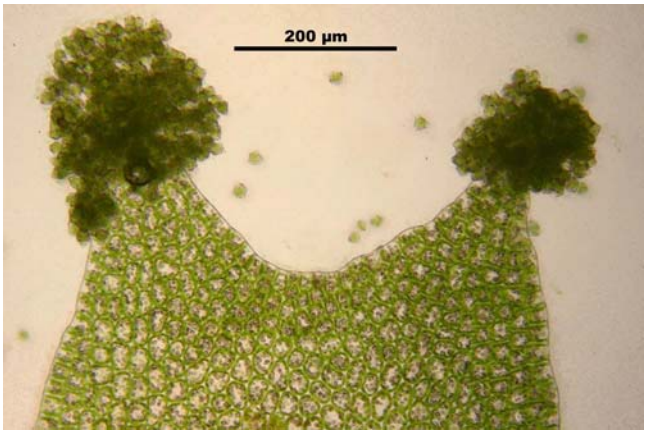

Figure 115. ***Lophozia ventricosa*** leaf showing gemmae at the tips of the leaf lobes. Photo by Hermann Schachner, through Creative Commons.

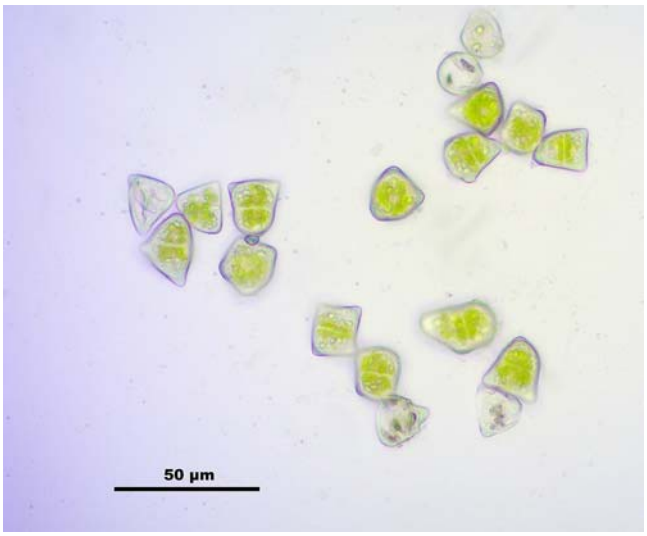

Figure 116. ***Lophozia ventricosa*** gemmae. Photo by Hermann Schachner, through Creative Commons.

Figure 117. ***Lophozia ascendens*** with gemmae, a species that produces gemmae later than do ***L. ventricosa*** and ***L. longifolia***. Photo by Michael Lüth, with permission.

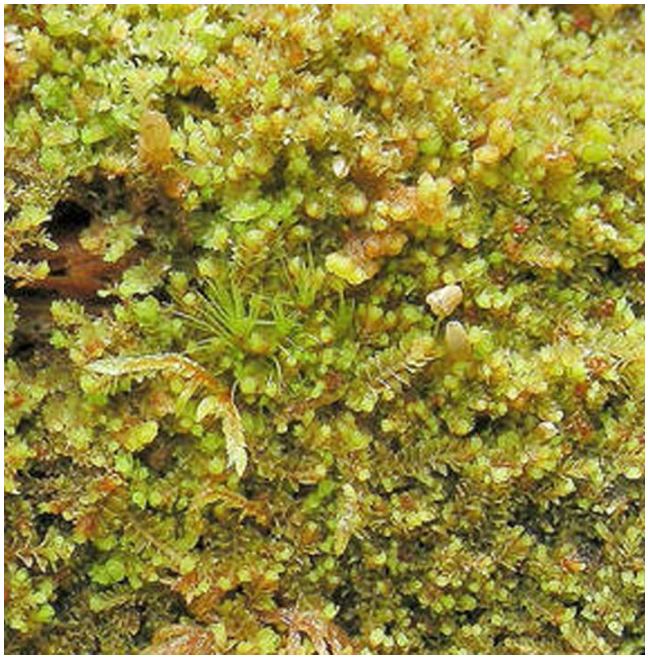

Figure 118. ***Lophozia longiflora***, a species that has earlier gemma production compared to ***L. ventricosa***. Photo by Earth.com, with permission.

Lophozia ventricosa (Figure 112-Figure 116) is a common liverwort in the National Nature Reserve in the Sumava Mountains, Bohemian Forest, Czech Republic. Holá *et al*. (2011) found that gemma production of the rare ***L. ascendens*** (Figure 117) was delayed in the growing season when compared to the more common ***Lophozia ventricosa*** and ***L. longiflora*** (Figure 118). The researchers concluded that air humidity was an important factor in the germinability of these gemmae. Gemma germination was low in early spring, reaching its highest level in August and September, and decreasing slightly in October. The researchers suggested that the rather mild winters of the Czech Republic assure a lower mortality of shoots in winter, thus decreasing selection pressure toward production of dormant gemmae of these species.

Fungal Interactions

Like many liverworts, ***Lophozia ventricosa*** (Figure 112-Figure 116) associates with members of the **Ascomycota** fungus ***Sebacina vermifera*** (see Figure 13) species complex (Bidartondo & Duckett 2010). It is known to share identical ***Sebacina vermifera*** DNA with the fungus on the leafy liverwort ***Nardia scalaris*** (Figure 119).

Biochemistry

Lophozia ventricosa (Figure 112-Figure 116) most likely benefits from its antimicrobial activity (Bukvicki *et al*. 2015). This species proved to have a number of compounds that are active against a variety of bacteria and fungi.

Figure 119. ***Nardia scalaris***, a leafy liverwort species that shares the fungus ***Sebacina vermifera*** having the same DNA as that fungus occurring on ***Lophozia ventricosa***. Photo by Hermann Schachner, through Creative Commons.

Lophozia ventricosa (Figure 112-Figure 116) possesses a variety of secondary compounds (Lu *et al*. 2005). The essential oils include sesquiterpenoids (Lu *et al*. 2005; Song *et al*. 2007) and terpenoids (Tori *et al*. 1993). Thus far, we have little information on the advantage these compounds give to specific liverworts, but it is likely that at least some of them serve as antiherbivore compounds. This is beneficial for organisms with slow growth rates, where the rate of herbivory could be greater than the growth rate. These antifeedant compounds could help the liverwort win the race.

Lophozia wenzelii (Figure 120-Figure 121)

Distribution

Lophozia wenzelii (Figure 120-Figure 121) is an arctomontane species (Bakalin 2004) distributed in Europe, Asia, and North America from Alaska, through the continental USA (ITIS 2020f). It extends from Greenland to India, China, and Japan in the Eastern Hemisphere, and to New Mexico, USA, in the Western Hemisphere (GBIF 2020c). It is unknown in the high Arctic except for Greenland (Bakalin 2004).

Figure 120. ***Lophozia wenzelii***, an arctomontane species that can occur in alpine streams, mountain bogs, and marshy areas. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Váňa (2005) considers that this species occurs mostly in mountain bogs and marshy areas. It occurs more rarely on wet rocks or rock debris. But in the Swiss Alps, Geissler (1976) found it in alpine streams, occurring uncommonly with ***Carex goodenoughii*** and ***Eleocharis quinqueflora*** (Figure 76) (Geissler & Selldorf 1986). In Russia at the Ushkovskii Volcano, Bakalin (2005) ***Lophozia wenzelii*** (Figure 120-Figure 121) occurs in glacial areas on stones of stream banks as well as on light soil between hummocks. This hummock soil is mixed yearly by freezing and thawing dynamics.

Figure 121. ***Lophozia wenzelii*** showing its growth habit. Photo by Štěpán Koval, with permission.

Bakalin (2005) reports that ***Lophozia wenzelii*** (Figure 120-Figure 121) grows among mosses and liverworts, but rarely forms pure **mats**. In moss tundra and oligotrophic bogs it is interspread within the boreal forest zone. In rare circumstances it grows along the peaty banks of streams on fine-granulated soil or on somewhat dry rocks. In the tundra it is able to grow in microdepressions between heath-lichen or moss patches. Frequently it occurs in wet (var. ***wenzelii***) or dry (var. ***groenlandica***) crevices of gravelly barrens and rocks (including seacoast cliffs). The main habitats, however, are oligotrophic bogs, where ***L. wenzelii*** sometimes grows in pure mats or mixed with ***Gymnocolea inflata*** (Figure 17-Figure 22), ***Scapania*** spp. (most frequently with ***S. paludicola*** – Figure 122), ***Cephalozia*** spp. (Figure 45-Figure 60), and ***Odontoschisma fluitans*** (Figure 92-Figure 93) (Bakalin 2004).

Figure 122. ***Scapania paludicola***, a species that often accompanies ***Lophozia wenzelii***. Photo by Michael Lüth, with permission.

In the Upper Puiva River in the Urals of Russia, Konstantinova and Lapshina (2017) found ***Lophozia wenzelii*** (Figure 120-Figure 121) on soil and bare loamy soil of the tundra, in snowbed communities, between boulders in rock fields, in dwarf shrub-sedge-***Sphagnum*** bogs, in seepages, on banks of brooks, and on road sides. Here they occur in pure mats or mixed with a variety of other leafy liverworts and mosses.

Adaptations

In Europe and northern Asia, var. ***litoralis*** exhibits rusty brown to red-brown plants. These live in places with disturbed vegetation cover, on soil near brook banks, or in the subalpine belt on mountains. Where vegetation is disturbed they occur on finely granulated soil or among mosses in lax **mats**. The occurrence on wet cliffs is rare.

Lophozia wenzelii (Figure 120-Figure 121) is a critically endangered species in the Czech Republic (Čihal & Kaláb 2017). In a model to determine the most important habitat characters for their presence, several factors emerged. The probability of presence is lower when the temperatures are higher in the warmest month. Higher precipitation values in the driest month also favor habitation. Since the least precipitation in the Czech Republic occurs in winter (January or February), the winter precipitation is important.

Lophoziopsis excisa (Figure 123-Figure 124)

(syn. = *Lophozia excisa*)

Distribution

Lophoziopsis excisa (Figure 123-Figure 124) is a highly variable and wide-ranging species (Schuster 1969). Its distribution is bipolar, ranging from Greenland southward to Italy and Spain in the Eastern Hemisphere and to some of the mountain forests in the southern Appalachian Mountains in eastern USA and to California in western USA. It has been found on Antarctica, in New Zealand, southern Chile, and southern Argentina. GBIF (2020d) includes it in Northern Asia as well, probably in alpine regions of Japan (Kitagawa 1965).

Figure 123. ***Lophoziopsis excisa*** with gemmae, a bipolar species extending south into mountains of the temperate zone. It most commonly occurs with other bryophytes on cliffs along streams and in bogs. Photo by Štěpán Koval, with permission.

Figure 124. ***Lophoziopsis excisa*** with gemmae. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

The habitats of this species suggest that it is indifferent to *p*H within most of the normal range (Schuster 1969). It occurs primarily on mineral substrata, but is also able to live on exposed loamy, acid soil. It is always mixed with other bryophytes, especially other leafy liverworts, in the Upper Puiva River basin of the Ural Mountains in Russia (Konstantinova & Lapshina 2017). Geissler and Selldorf (1986) found it was uncommon with *Carex goodenoughii* in bogs in Ticino, Switzerland. In ***Rhododendron lapponicum*** (syn. = *Ledum groenlandicum*; Figure 125) bogs of the glacial relict lake areas of the Komi Republic of northwestern Russia, it occurs on decaying wood and slightly matted soil, and on soil in a ***Menyanthes-Comarum Sphagnum*** mixed forest (Dulin 2015). In the

Timpton River Basin, South Yakutia, Russia, Sofronova (2017) found ***Lophoziopsis excisa*** (Figure 123-Figure 124) mixed with other liverworts on soil of moist south-facing cliffs along the river bank as well as on fine soil in cliff cracks. But it is also found on soil in between stones of the stone field on south-facing slopes, where it can occur in pure mats or mixed with other liverworts.

Figure 125. ***Rhododendron groenlandicum*** bog, a habitat where it occurs on decaying wood and slightly matted soil in northwestern Russia. Photo by Wynn Anderson, through Creative Commons.

Reproduction

Lophoziopsis excisa (Figure 123-Figure 124) is **paroicous** with red gemmae (Konstantinova & Savchenko 2018).

Fungal Interactions

Newsham and Bridge (2010) noted the presence of fungi belonging to **Sebacinales** (Figure 13) in ***Lophoziopsis excisa*** (Figure 123-Figure 124) at Léonie Island in the southern maritime Antarctic. Newsham *et al*. (2014) reported the occurrence of ***Cladophialophora*** (Figure 126) and related fungi in the tissues of ***Lophoziopsis excisa*** from Léonie Island. Fungal partners are fairly well known among bog plants (Thormann 2006), including liverworts (Duckett & Clymo 1988) so the presence of fungi with this liverwort species on peaty soils is not surprising.

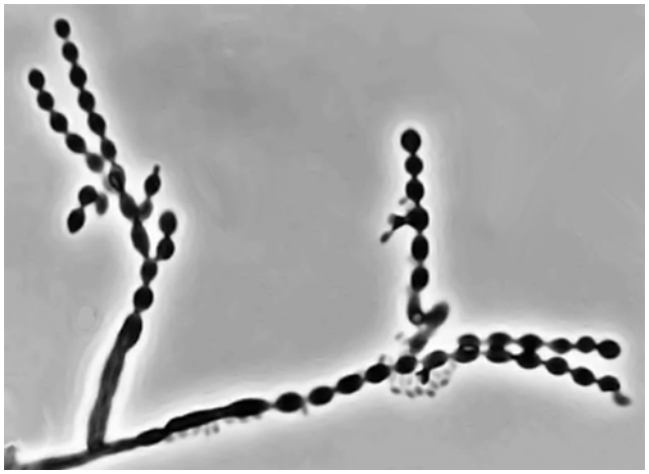

Figure 126. ***Cladophialophora*** sp.; some species of this fungal genus are found in tissues of ***Lophoziopsis exicisa***. Photo by Medmyco, through Creative Commons.

Trilophozia quinquedentata (Figure 127-Figure 128)

(syn. = *Tritomaria quinquedentata*)

Distribution

Trilophozia quinquedentata (Figure 127-Figure 128) is widely distributed in the Northern Hemisphere from the Arctic to northern USA and to at least one location each in China and Japan (TROPICOS 2020).

Figure 127. ***Trilophozia quinquedentata***, a Northern Hemisphere mostly terrestrial species that can occur on wet cliffs, dripping rock surfaces, and associated with waterfalls. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

This mostly terrestrial species is at least tolerant of water, occurring on wet cliffs of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002). It also occurs on dripping steep rock surfaces of granite at the margins of shaded permanent waterfalls, where it is only loosely attached (Figure 128) (Vieira *et al*. 2005). It is also typically associated with ***Chiloscyphus polyanthos*** (Figure 129) and ***Aneura pinguis*** (Figure 130) in mountain streams of northwest Portugal.

Figure 128. ***Trilophozia quinquedentata*** loosely attached to its substrate. Photo by Hugues Tinguy, with permission.

Figure 129. ***Chiloscyphus polyanthos***, a common associate of ***Trilophozia quinquedentata***. Photo by Štěpán Koval, with permission.

Figure 130. ***Aneura pinguis***, a common associate of ***Trilophozia quinquedentata***. Photo by Hermann Schachner, through Creative Commons.

Tritomaria exsecta (Figure 131-Figure 136)

(syn. = *Sphenolobus exsectus*)

Distribution

Tritomaria exsecta (Figure 131-Figure 136) extends in a wide range including Australiia, Asia, Europe, and North America from Mexico to Alaska (ITIS 2020g). It has also been reported from eastern Africa (BFNA 2020) and New Zealand (Engel 2006).

Aquatic and Wet Habitats

Its inclusion in aquatic and wetland studies seems to be rare. Nichols (1916) reported it as a **calciphobic** (avoiding calcium) species along rivers in Connecticut, USA. Glime (1982) reported it from the wall of the humid flume (Figure 37) at Franconia Notch, New Hampshire, USA.

Figure 131. ***Tritomaria exsecta***, a wide-ranging mostly terrestrial species, occurring as a calciphobe along rivers and on humid canyon walls. Photo by Hermann Schachner, through Creative Commons.

Figure 132. ***Tritomaria exsecta***. Photo by Michael Lüth, with permission.

Reprodution

It forms mats and can produce apical gemmae (Figure 133-Figure 136).

Figure 133. ***Tritomaria exsecta*** in a mat with gemmae at the apex of shoots. Photo by Hermann Schachner, through Creative Commons.

Figure 134. ***Tritomaria exsecta*** with apical gemmae. Photo by Michael Lüth, with permission.

Figure 135. ***Tritomaria exsecta*** with gemmae. Photo by Michael Lüth, with permission.

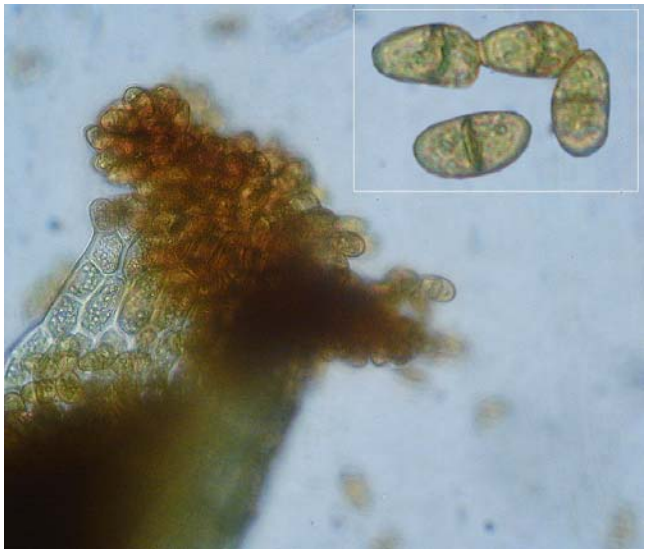

Figure 136. ***Tritomaria exsecta*** gemmae. Photo by Michael Lüth, with permission.

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143)

Distribution

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143) is an Arctic-alpine, circumboreal species (Harpel & Dewey 2005). It is distributed in North America from Greenland and Alaska southward to Colorado, Iowa, Michigan, and Pennsylvania in the USA, It is also present in Europe, Asia, and Africa (Hong 2002).

Figure 137. ***Tritomaria exsectiformis***, a species distributed from the Arctic to the temperate region in the Northern Hemisphere, occurring mostly at high elevations where it often occurs in areas of perennial flow at or near springs and seeps. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

In Greenland, Hassel *et al.* (2014) found ***Tritomaria exsectiformis*** (Figure 137, Figure 141-Figure 143) growing on rocks in a heathland of ***Vaccinium uliginosum*** (Figure 138) with the mosses ***Saelania glaucescens*** (Figure 139), ***Bartramia ithyphylla*** (Figure 140), and liverwort ***Scapania*** sp. (*e.g.* Figure 122).

Figure 138. ***Vaccinium uliginosum*** with fruit, the dominant species in heathland where one can find ***Tritomaria exsectiformis***. Photo by David Gaya, through Creative Commons.

Figure 139. ***Saelania glaucescens***, a species growing with ***Tritomaria exsectiformis*** on rocks in blueberry heathlands. Photo by Michael Lüth, with permission.

Figure 140. ***Bartramia ithyphylla***, a species growing with ***Tritomaria exsectiformis*** on rocks in blueberry heathlands. Photo by J. C. Schou, with permission.

In western USA, Harpel and Dewey (2005) found ***Tritomaria exsectiformis*** (Figure 137, Figure 141-Figure 143) to be typical of open to shaded coniferous forest where it is associated with low volume, perennial water flow at or near springs and seeps. These typically occur on very gentle topographic gradients. Its substrate is usually decaying wood (Figure 141) in stage four decay and having direct contact with water. It is never present where there is high volume flow.

Figure 141. ***Tritomaria exsectiformis*** on wet, decaying wood. Photo by Stan Phillips, through public domain.

Reproduction

This perennial species occurs mostly at high elevations where snow remains a long time into spring and summer, usually at elevations above 1500 m (Harpel & Dewey 2005). This gives it a short growing season with a late summer and fall. Reproduction occurs only by gemmae (Figure 142-Figure 143) and other vegetative means. The species is a restricted terrestrial associated with the montane streams and streambanks of western Canada (Figure 103) (Vitt *et al.* 1986; Glime & Vitt 1987). Hong (1994) reported it from creek banks, decayed wood, and humus over decayed wood in forests ranging from 0 to 2300 m asl.

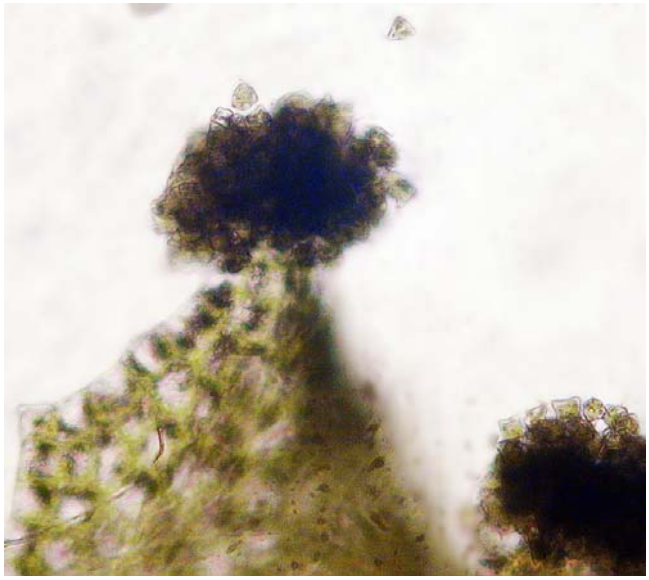

Figure 142. ***Tritomaria exsectiformis*** with clusters of gemmae on leaf tips. Photo by Michael Lüth, with permission.

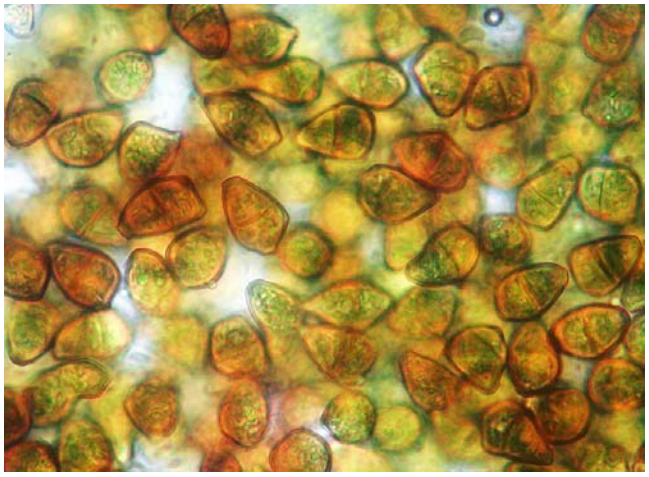

Figure 143. ***Tritomaria exsectiformis*** gemmae. Photo by Michael Lüth, with permission.

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143) is dioicous, thus rarely producing sporophytes. Harpel and Dewey (2005) suggested that dispersal is most likely accomplished by moving water and possibly invertebrates. It requires a substrate that provides a constant water supply without the dangers of scouring.

Summary

The **Cephaloziineae**, except for **Scapaniaceae**, are not common in wet habitats, and especially rare in the water. The **Adelanthaceae** has only 2 species in 2 genera that have appeared in wetland habitats, with ***Syzygiella sonderi*** being submerged in high elevation lakes in the Andes. The **Anastrophyllaceae** is predominantly terrestrial, but may appear on wet cliffs and wet rocks of stream banks and waterfalls. I have identified only 9 species (7 genera) in such wet habitats. The mostly tiny **Cephaloziaceae** seem somewhat more aquatic, occurring in small ponds and mires as well as wet cliffs and rocks of lake shores and stream banks, but with only 9 species (3 genera) included in the literature surveyed. They often occur among other bryophytes, thus protecting the from frequent desiccation. Some become submerged. Some species regenerate from buried stolons. The **Ascomycota** ***Mniaecia jungermanniae*** can inhabit members of ***Cephalozia***, and ***Pezoloma ericae*** can occur on the rhizoids. The **Zygomycota** species ***Mucor rhizophilus*** occurs on rhizoids in several genera of **Cephaloziaceae**. The **Cephaloziellaceae** is represented by 8 species (2 genera) in carpets of wet areas in the Antarctic and lakes of Finland, but it is mostly terrestrial. The **Lophoziaceae** is represented by 6 species (2 genera) here, again by species that grow mostly terrestrially. Nevertheless, some occur in mountain lakes and others in bogs and marshy areas. Seeps and dripping rock surfaces are suitable for some. Some take advantage of the water from late snow melt.

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